UNIVERSITY OF MICHIGAN
JAN 7 - 1959
MUSEUMS LIBRARY

VOLUME 131 PART 4 DECEMBER 1958

PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY

OF

LONDON

LONDON
PUBLISHED BY THE SOCIETY
SOLD AT ITS HOUSE IN REGENT'S PARK, LONDON, N.W.1

Price Thirty Shillings

THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.
Clerk of Publications . . . G. B. STRATTON, M.B.E.

The **Proceedings,** founded in 1830, are published in royal octavo form and constitute the principal organ of the Society for the publication of original works in zoology, and for notices of the business transacted at the Scientific Meetings of the Society.

Two volumes are published annually; each volume containing four numbers. Price per volume £6; separate numbers £1 10*s.* 0*d.* each.

The **Transactions,** founded in 1833, are published in quarto form and contain those papers and monographs which by reason of the size of the illustrations, are better adapted for publication in that format. The " Transactions " are published at irregular intervals at prices varying in accordance with the cost of production.

OTHER PUBLICATIONS OF THE SOCIETY.

The Zoological Record, founded in 1864, is issued annually with the object of providing a complete list of references to publications in zoology in all its branches for each year of issue, the price of the complete volume is £8. The Society is unable to supply *complete sets* of the " Record " as several volumes are now out of print. The following volumes are available :—

Vols. 65–71 (1928–1934), 85 (1948) at £5 each.
Vols. 86–91 (1949–1954) at £6 each.
Vol. 92 (1955) at £8.

PHOTOLITHOGRAPH REPRINT. Vols. 1–20 (1864–1883). Obtainable only from Messrs. Butterworths, 88 Kingsway, London, W.C.2.

Complete set of 20 volumes, bound in cloth, price £160.
Complete set of 20 volumes, in paper covers, price £155.
Separate volumes, in paper covers, at £8 each.

Nomenclator Zoologicus. The five volumes contain the names of all the genera and subgenera in zoology from the 10th Edition of Linnaeus 1758 to the end of 1945, with a bibliographical reference to the original description of each. Price 17½ guineas, postage extra. Price of the separate volumes: Vols 1–4 (1758–1935); Vol. 5 (1936–1945) 3½ guineas each, postage extra.

Advice on Pets. Price 1*s.*, postage extra.

Centenary History of the Zoological Society of London, by P. Chalmers Mitchell. 1929. Price 10*s.*, postage extra.

Index to Sir George Hampson "A revision of the subfamily Pyraustinae and family Pyralidae " published in the 'Proceedings' 1898 and 1899. Price 10*s.* 6*d.* post free.

Some Suggestions on the Transport of Animals. Price 1*s.* 6*d.*, post free.

" Zoo "—The official guide to the London Zoological Gardens. Price 2*s.* 6*d.*, postage extra.

All communications concerning the Society's publications should be sent addressed to:

THE SCIENTIFIC DIRECTOR,
ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W.1,
ENGLAND.

THE STOMACH IN THE EULAMELLIBRANCHIA ; STOMACH TYPE IV

BY

R. D. PURCHON, PH.D., F.L.S.

Raffles Professor of Zoology, University of Malaya, Singapore

[Accepted 11th February 1958]

(With 14 figures in the text)

CONTENTS

	Page
Introduction	487
Stomach Type IV	488
Definition of type	488
Description of material	489
Discussion	517
Summary	524
References	524
Key to the lettering of the figures	525

INTRODUCTION

The structure and function of the stomach has previously been described for the Protobranchia and Septibranchia (Purchon, 1956), and for the Filibranchia and Pseudolamellibranchia (Purchon, 1957), and references to previous literature were given in the first of these papers. It now remains to treat with the stomach in the fifty-four families in the Eulamellibranchia (Thiele, 1934). Information is now available for some forty of these families, and it has been been found that they fall into two distinct categories as regards the internal structure of the stomach, approximately half possessing a stomach of Type IV, comparable in every way with that already described for certain Filibranchia and Pseudolamellibranchia (Purchon, 1957). These seventeen families are considered in the present paper.

Specimens of *Anodonta, Sphaerium, Astarte, Montacuta, Thyasira* and *Lucinoma* were studied at the Department of Zoology, University of Bristol, the first genus having been obtained through commercial sources, the second from the Fresh water Biological Station at Wray Castle, and the remainder from the Laboratory of the Marine Biological Association at Plymouth. The writer is particularly grateful to Professor J. E. Harris, F.R.S. for his kindness in providing laboratory facilities in his Department in the summers of 1955 and 1957, without which this work could not have been completed.

Specimens of *Pandora* were studied at the Stazione Zoologica at Naples in June 1955, when the writer occupied the research table of the Royal Society. *Hiatella* was studied at Millport in September 1955. The writer wishes to record his thanks to the Royal Society for permission to use their research table at Naples, and for financial assistance from the Browne Research Fund

for the periods of research at Naples and at Millport. Thanks are also due to the Directors and staff of each of these marine biological stations for their courteous and unfailing help. The remainder of the material was studied at the Department of Zoology, University of Malaya, Singapore.

Specimens of *Cleidothearus* and of *Velesunio* were sent by air to Singapore in a vacuum flask by Miss J. Hope Macpherson, National Museum of Victoria, Melbourne. The specimens arrived in a healthy state, and grateful thanks are due to Miss Macpherson for this invaluable help, and also for identifying the material.

Specimens of *Anodonta*, *Astarte*, *Sphaerium*, *Hiatella*, *Beguina*, *Scintilla*, *Chama*, *Laternula* and *Pandora* were identified by Professor R. Tucker Abbott, Academy of Natural Sciences, Philadelphia. Specimens of *Montacuta*, *Thyasira*, and *Lucinoma* were identified by Miss D. Atkins, Dr D. B. Carlisle and Dr G. M. Spooner, at the Laboratory, Citadel Hill, Plymouth. The writer wishes to record his appreciation of this expert help.

Thanks are especially due to Mr G. Owen, Department of Zoology, University of Glasgow, for his generosity in permitting the writer to include in this paper the description and illustration of the interior of the stomach of *Myadora ovata*. This work was carried out by Mr Owen in New Zealand and was transmitted to the present writer in a personal communication.

STOMACH TYPE IV

Purchon (1957) found that Stomach Type IV occurred in four families in the Filibranchia and Pseudolamellibranchia, namely the Trigoniidae, Limidae, Pectinidae and Anomiidae. Examples were described and on the basis of these descriptions a definition was given for Stomach Type IV. It was mentioned that in many families in the Eulamellibranchia the stomach was similar in appearance. In the present paper these examples are described in detail, careful comparisons have been made, and it has been concluded that all of these should be assigned to Stomach Type IV. The number of families known to possess Stomach Type IV has been increased from four to twenty-one, and it is now found that the original definition is inadequate. A new definition is therefore now provided, covering all families concerned, and superseding the previous description.

Definition of Type

1. The oesophagus enters on the anterior side of the stomach.

2. The style-sac and mid-gut are usually conjoined (the Anomiidae, Erycinidae, Montacutidae and Cyamiidae are exceptional) and leave the ventral or posterior wall of the stomach.

3. There is a crystalline style which projects across the stomach, presses into the mouth of the dorsal hood, and probably rotates in a clockwise direction when viewed from the anterior end.

4. The dorsal hood is relatively large and there is usually a well developed sorting area on its anterior face (the dorsal hood is small in the Montacutidae and is apparently absent in the Cyamiidae). The mouth of the dorsal hood is invested by lobes of the gastric shield.

5. The minor typhlosole terminates on the right wall of the stomach, close to the orifice of the mid-gut. (The minor typhlosole appears to be absent in the Anomiidae, Erycinidae and Montacutidae).

6. The major typhlosole passes forwards from the mid-gut into the stomach, accompanied on its right side by the intestinal groove (The condition in the Pandoridae is as yet uncertain). Both structures curve to the left and terminate on the left anterior floor of the stomach within or close to the mouth of the left pouch (In the Unionidae, Chamidae and Gastrochaenidae both structures penetrate deeply into a deep pocket on the left anterior floor of the stomach). The major typhlosole does not possess a tongue, nor does it invade any of the orifices of the ducts from the digestive diverticula on the anterior or right side of the stomach. (In the Carditidae the major typhlosole and intestinal groove terminate in a large tight spiral on the anterior floor of the stomach).

7. There is a left pouch on the anterior wall of the stomach, the upper or posterior border of this pouch being invested by a lobe or rim of the gastric shield. (The Unionidae and Lucinidae are exceptional). This left pouch receives one or more ducts from the digestive diverticula on the left side of the body. (This is not true for the Astartidae, Pandoridae or Laternulidae). The pouch may be deep and compact with the ducts from the digestive diverticula entering its depths, or the pouch may be flattened and extended, the ducts opening at some distance from that part of the pouch which is invested by the gastric shield. (No left pouch has been found in the Cyamiidae or in the Ungulinidae ; it is not known whether any ducts enter the left pouch in the Montacutidae).

8. The food-sorting caecum may be large, with a well developed sorting area on the anterior or right wall of the stomach, e.g. the Pectinidae, Limidae, Myochamidae and Chamostreidae ; this condition may be primitive. The food-sorting caecum and the sorting area may be somewhat reduced, e.g. the Anomiidae, Chamidae, Pandoridae and Laternulidae ; alternatively it may be unrecognisable, as in all other families.

9. In addition to the ducts which enter the left pouch, the remainder of the ducts from the digestive diverticula open on to the anterior and right walls of the stomach. Their orifices may be numerous and scattered (e.g. the Pectinidae, Anomiidae, Chamidae and Carditidae) ; this condition may be primitive. The orifices may be clustered (e.g. the Limidae and Erycinidae), or they may open into the stomach via a small number of embayments of the stomach wall.

Description of Material

UNIONACEA

Unionidae

Anodonta cygnea (L.) (Fig. 1)

The interior of the stomach of *A. cygnea* has been figured and described by Graham (1949), who referred to previous work on *A. cellensis* by Gutheil (1912). The present description differs from that of Graham (1949) only in

matters of proportion and in the inclusion of some further details. There are considerable differences, however, in questions of interpretation and nomenclature between the present account and that of Graham (1949), who had studied no other eulamellibranch with this type of stomach.

The interior of the oesophagus is longitudinally grooved ; it enters the anterior face of the stomach (O), its termination being indicated by a well defined transverse rim (RM). The combined style-sac (SS) and mid-gut leave the stomach postero-ventrally. The minor typhlosole (MT) passes forwards for a short distance, it then turns sharply upwards and terminates low down on the right side of the stomach. The major typhlosole passes forwards over the floor of the stomach, curving gradually to the left, and finally disappearing into a large aperture which lies anteriorly on the left wall of the stomach (DDD^1) and into which open five ducts from the digestive diverticula on the left side of the stomach. The major typhlosole terminates outside the mouth of the posteriormost of these ducts from the digestive diverticula. Cilia on the major typhlosole and posterior to it beat inwards, while the cilia of the intestinal groove beat outwards.

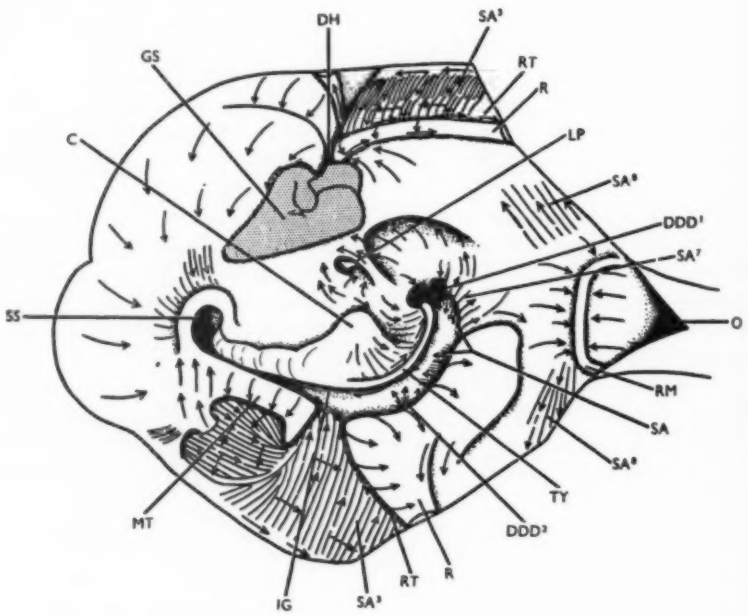


Fig. 1.—*Anodonta cygnea* L. The interior of the stomach, seen from the right side after a mid-dorsal incision through the roof. × about 6. (For lettering see p. 525).

There is a well developed dorsal hood (DH) on the left side of the stomach. Its anterior wall bears a large sorting area (SA^3) of transverse ridges and grooves, which extends over the roof of the stomach and down its right side. Cilia on the crests of the ridges of this sorting area beat transversely over the

crests and convey particles towards and into the dorsal hood. There is also a longitudinal current along the dorsal and posterior border of the sorting area which similarly directs material into the dorsal hood. Cilia in the grooves of the sorting area beat along the grooves and pass material into a rejection tract (RT) which passes along the anterior margin of the sorting area and discharges waste material into the intestinal groove (IG). Ventral to this rejection tract there is a longitudinal ridge (R) which passes over the roof of the stomach and down the right wall of the stomach between the above mentioned sorting area and the orifice of the oesophagus. There is an ill-defined system of parallel ridges on the anterior roof of the stomach (SA^8), on which cilia beat backwards and convey particles towards the dorsal hood.

Immediately below the mouth of the dorsal hood there is a small left pouch (LP) into which open two ducts from the digestive diverticula. In front of the left pouch there is a broad shallow hollow in which cilia beat backwards and upwards. The gastric shield (GS) is relatively small ; it lies on the left wall of the stomach, below the mouth of the dorsal hood into which it only sends a small flare. The gastric shield does not reach the rim of the left pouch. A prominent cusp on the gastric shield projects into the lumen of the stomach.

There is a sorting area of broad irregular folds on the anterior floor of the stomach (SA^7) on which cilia beat anteriorly towards the orifice of the oesophagus.

There is an ill-defined sorting area low down on the anterior face of the stomach, consisting of slender parallel ridges and grooves (SA). Cilia on the crests of the ridges beat transversely over the crests to the left, towards the orifice into which the major typhlosole passes and into which ducts from the digestive diverticula open (DDD^1). Cilia in the grooves of this sorting area beat along the grooves and into the intestinal groove (IG). An isolated part of this sorting area passes into the orifice into which the major typhlosole passes (DDD^1).

In addition to the two groups of ducts from the digestive diverticula which open on the left side of the stomach (LP, DDD^1), two ducts enter the stomach from the digestive diverticula on the right side of the stomach. The orifices of these ducts lie anteriorly on the right side of the floor of the stomach, close to the intestinal groove, the anterior duct (DDD^2) being large and the posterior duct being small. The latter is not shown in the figure (Fig. 1).

On the floor of the stomach there is a conspicuous conical mound (C) which may normally press against the anterior border of the mouth of the dorsal hood, and against the thick ridge which passes down the right side of the stomach, thus dividing the interior of the stomach into separate anterior and posterior compartments.

Graham (1949) considered the possible homologies of the apertures into which the ducts from the digestive diverticula open (LP, DDD^1, DDD^2). He suggested two alternative interpretations : the orifice on the right anterior wall (DDD^2) is either homologous with the isolated orifices of ducts from the digestive diverticula which occur on the right posterior wall in some genera, or it is homologous with the " right half of the caecum ", a structure

which he considered to be typical of the Eulamellibranchia, into which open a number of ducts from the digestive diverticula and into which penetrates a tongue of the major typhlosole. He considered the latter interpretation to be improbable since it would have required the abortion of the " right half of the caecum " as defined above. The force of this argument is reduced now that it is known that the condition described above is true not only for *Anodonta*, but also for at least seventeen families or twelve orders in the Eulamellibranchia.

Hyridellidae

Velesunio ambiguus Philippi (=*Hydridella australis* Lam.)

This species, erroneously placed in the Mutelidae by Thiele (1934), has been placed in the Unionidae, but more recently in the Hyridellidae (personal communication from Miss J. Hope Macpherson). The interior of the stomach is remarkably similar to that of *Anodonta cygnea* as figured and described above, and no illustration of the stomach of *Velesunio* is necessary. This similarity is particularly remarkable in view of the long period of time in which the fresh waters of Australia have been isolated from those of Europe and Asia. Evidently the internal structure of the stomach is of high stability in the Unionacea.

ASTARTACEA

Astartidae

Astarte sulcata da Costa (Fig. 2)

The oesophagus (O) enters the stomach antero-dorsally and the combined style-sac (SS) and mid-gut leave the stomach postero-ventrally. The minor typhlosole (MT) terminates at the mouth of the mid-gut. The major typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards over the floor of the stomach, curving at first gently and then more abruptly to the left; it terminates a little to the left of the median line on the anterior floor of the stomach without having approached the orifices of any of the ducts from the digestive diverticula. The anterior face of the stomach, as also the left anterior side, overhangs the anterior part of the major typhlosole and intestinal groove.

The digestive diverticula on the left side of the stomach open into the stomach by two ducts (DDD^1), the orifices of which are situated to the left of the termination of the major typhlosole and intestinal groove, and under the above mentioned overhang of the left anterior stomach wall. The digestive diverticula of the right side open into the stomach by a single duct (DDD^2) at the right extremity of this overhang.

The dorsal hood (DH), which is relatively small, arises on the left side of the roof of the stomach and curves downwards to the left. There is one longitudinal ridge on the posterior wall, and two on the anterior wall, but there is apparently no ridged sorting area in the dorsal hood.

The left pouch (LP) is a broad hemispheric pocket which lies on the left wall of the stomach, below and in front of the mouth of the dorsal hood. No ducts enter the left pouch from the digestive diverticula. There is a gastric

shield (GS) of relatively small size, which invests the mouth of the dorsal hood with a saddle-shaped lobe and which provides a rim to the posterior border of the left pouch.

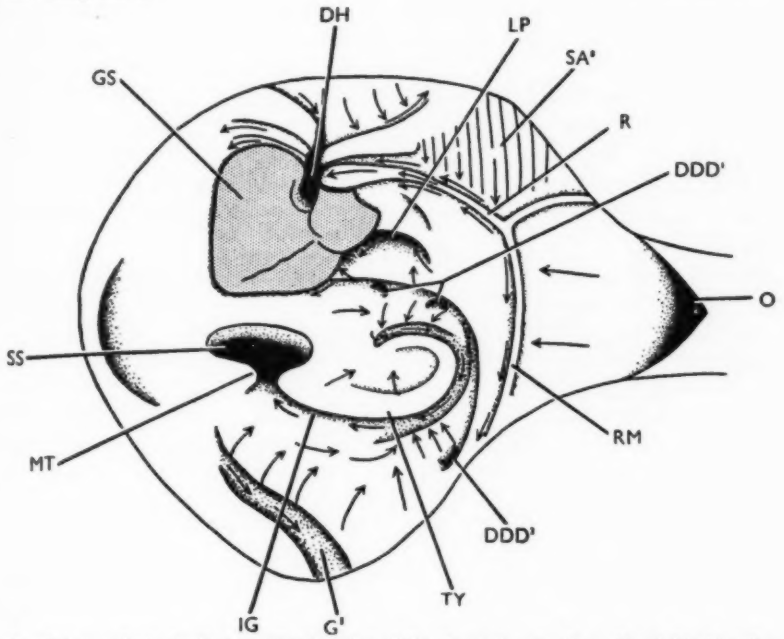


Fig. 2.—*Astarte sulcata* da Costa. The interior of the stomach, seen from the right side after a mid-dorsal incision through the roof. (For lettering see p.525).

The orifice of the oesophagus is marked by a rim (RM), from the left corner of which a ridge (R) passes backwards over the left anterior wall and into the dorsal hood. Material entering the stomach from the oesophagus is diverted by the rim and is passed by ciliary currents along the ridge and into the dorsal hood. The only sorting area noted (SA^s) lies on the roof of the stomach anteriorly, and it serves to collect particles and direct them towards the dorsal hood.

On the right side of the stomach there is a broad, ill-defined groove (G^1) in which cilia beat upwards and into the dorsal hood.

The epithelium underlying and in the vicinity of the gastric shield is dark green in colour. In general the stomach wall is thin and transparent, and difficulty was experienced in determining some of the above mentioned details.

CARDITACEA

Carditidae

Beguina semiorbiculata L. (Fig. 3)

The specimens studied were found deeply embedded in massive corals a little below low water mark of spring tides, at Raffles Lighthouse, Singapore. Living specimens were collected and were studied immediately.

The oesophagus (O) is short and wide and enters the stomach antero-dorsally. The combined style-sac (SS) and mid-gut leaves the stomach postero-ventrally, and the major typhlosole (TY) passes forwards from the mouth of the mid-gut across the floor of the stomach, and then turns sharply to the left and forms a tight spiral fold (SF) on the left anterior floor of the stomach. The major typhlosole is accompanied on its right side by the intestinal groove (IG) which penetrates to the apex of the spiral fold.

The gastric shield (GS) lies on the left side of the stomach and sends a flare deeply into the mouth of the dorsal hood (DH) which lies above. The mouth of the dorsal hood is wide, with a small horn (H) projecting posteriorly. The main part of the dorsal hood passes forwards above the left anterior roof of the stomach.

There is a left pouch (LP) on the left anterior wall of the stomach immediately below the dorsal hood ; five ducts from the digestive diverticula enter the left pouch, and its upper border is invested by a lobe of the gastric shield in the usual manner. There is a small sorting area (SA^6) in the left pouch. The remainder of the ducts from the digestive diverticula open into the stomach in two groups, four orifices lying on the left anterior wall (DDD^1) above the spiral fold, and four orifices lying antero-dorsally on the right wall of the stomach (DDD^2) near the mouth of the dorsal hood (in Fig. 3 one of these orifices is shown adjacent to the anterior border of the dorsal hood). The major typhlosole does not enter into relationship with any of these ducts from the digestive diverticula.

Material entering the stomach from the oesophagus will fall on to a sorting area composed of very fine folds which pass obliquely upwards and outwards (SA^7). This sorting area is separated from the orifice of the oesophagus by a well defined rim (RM). Such material is transported forwards and upwards to left and to right and is conveyed to the anterior border of the dorsal hood, into which it passes.

On the anterior side of the dorsal hood ciliary currents pass inwards (SA^8). Towards the apex of the hood there is a powerful inward dorsal current and a powerful outward ventral current. On anterior and posterior sides of the hood there are longitudinal ridges on which cilia beat upwards and into the longitudinal inward current. These currents ensure that particles will circulate for some time near the apex of the dorsal hood. On the posterior wall of the dorsal hood and near its mouth there are two longitudinal ridges separated by a sorting area (SA^5) composed of short transverse folds. Here the cilia beat obliquely backwards towards the stomach.

On the right side of the stomach there is a funnel shaped depression which passes downwards from the mouth of the dorsal hood. Cilia in this region beat away from the dorsal hood, past the mouths of a small number of ducts from the digestive diverticula, and reject material in a well defined rejection tract (RT) into the intestinal groove (IG).

In the mouths of the individual ducts from the digestive diverticula the cilia beat out of the ducts, towards the stomach. This is also true for the ducts opening on the left side of the stomach.

On the major typhlosole (TY) cilia beat upwards, away from the intestinal groove. On the spiral fold (SF) these transverse currents combine to form a rejection mechanism consisting of ciliary currents which pass radially inwards towards the apex of the spiral fold. Particles caught in this mechanism are ultimately deposited in the intestinal groove. The spiral fold of the major typhlosole is therefore regarded as a rejection mechanism, serving to protect the orifices of the ducts of the digestive diverticula from the approach of excessive quantities of particulate matter. A spiral fold with similar structure and function has been described for *Tridacna* (Purchon, 1955).

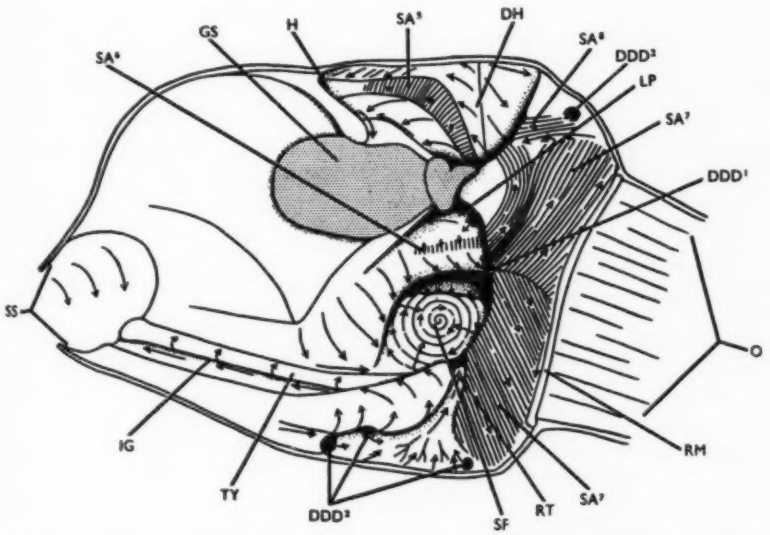


Fig. 3.—*Beguina semiorbiculata* L. The interior of the stomach after opening it by a mid-dorsal incision from the oesophagus to the style-sac. (For lettering see p. 525).

Nevertheless, some material may pass the spiral fold and approach the orifices of the ducts from the digestive diverticula lying on the adjacent wall of the stomach, and in the left pouch above. Such material comes under the influence of cleansing mechanisms which protect the orifices of the ducts. The lower border of the left pouch is indicated by a narrow horizontal sorting area (SA^6) composed of short transverse folds on which the cilia beat upwards into the left pouch. In the left pouch cilia beat strongly backwards towards the gastric shield, and material driven thither may then be collected by the revolving crystalline style. Below the horizontal sorting area (SA^6) ciliary currents on the left wall of the stomach pass downwards, towards the spiral fold and into the intestinal groove which circumnavigates it.

Pelseneer (1911) figured and described a spiral fold in the closely related *Cardita*, comparable with the spiral fold of the major typhlosole described here for *Beguina*.

CYRENOIDIDAE

Sphaeriidae

Sphaerium corneum L. (Fig. 4)

The oesophagus opens on the anterior face of the stomach by a relatively wide aperture (O). The combined style-sac and mid-gut (MG) leaves the posterior floor of the stomach, and the crystalline style (CS) projects vertically upwards into the stomach. The major typhlosole (TY) passes forwards and to the right over the floor of the stomach. It then curves in a semi-circle to the left and finally forms a comparable semi-circular projection on the left anterior floor of the stomach. The major typhlosole is accompanied throughout its course by the intestinal groove (IG) which originates on the median border of a large pocket on the left wall of the stomach. This pocket is the left pouch (LP), for its posterior border is invested by a lobe of the gastric shield (GS), and it receives three ducts (DDD^1) from the digestive diverticula of the left side of the body. The digestive diverticula of the right side open into the stomach by a single large aperture (DDD^2) on its right wall.

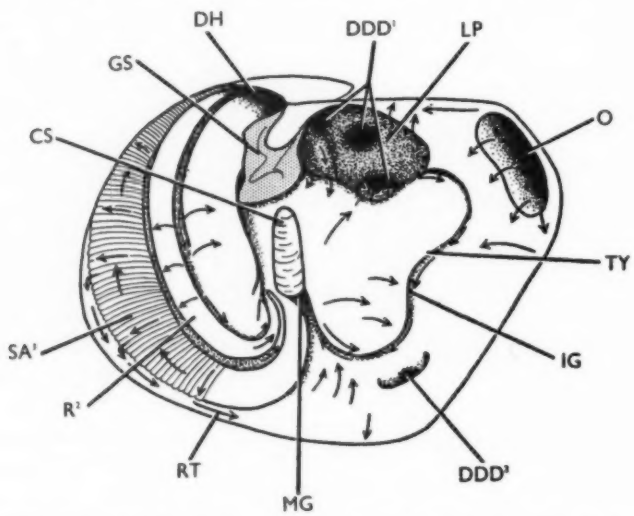


Fig. 4.—*Sphaerium corneum* L. Interior of the stomach, seen from above, after a mid-dorsal incision through the roof. × about 25. (For lettering see p. 525).

The dorsal hood (DH) lies on the posterior part of the roof of the stomach. It consists of a relatively small conical forward-projecting pocket which lies on the left posterior side of the stomach, but the posterior wall of the mouth of the dorsal hood is very large and extends over the posterior wall and on to the posterior part of the right side of the stomach. This region bears a well developed sorting area (SA^3) which passes towards the apex of the dorsal hood. There is a small gastric shield (GS) which lies between the mouths of the dorsal hood and of the left pouch, into each of which it sends investing flares.

Particles entering the stomach from the oesophagus are conveyed towards the mouth of the dorsal hood by ciliary currents on the roof and sides of the anterior part of the stomach. On the sorting area of the dorsal hood cilia beat transversely over the crests of the folds and towards the apex of the dorsal hood, while the cilia in the grooves between the folds beat along the grooves to the right and into a rejection current (RT) that empties on the right posterior side of the stomach. Ventral to the sorting area of the dorsal hood there is a well developed ridge (R^2) with a longitudinal groove on each side. On the ridge and in the two grooves cilia beat out of the dorsal hood and towards the mouth of the mid-gut (MG).

On the floor of the stomach cilia beat powerfully forwards. On the left side of the median line particles are carried towards the left pouch, while on the right side they pass slightly to the right and over the major typhlosole (TY). A large area on the posterior wall of the stomach, below the mouth of the dorsal hood, is apparently not ciliated.

CYAMIACEA

Cyamiidae

Turtonia minuta (Fabricius)

The systematic position of the genus *Turtonia* is dubious, Winckworth (1932) having placed it with *Lasaea* in the Erycinidae while Thiele (1934) placed it in the Cyamiidae. Oldfield (1955) concluded from a comparative study of *Turtonia* and *Lasaea* that these two genera should not be placed in the same family. In the present study, therefore, the classification of Thiele (1934) is followed.

The interior of the stomach of *Turtonia minuta* was figured and described by Oldfield (1955), the findings of whom are summarised as follows :—

The oesophagus enters the stomach antero-ventrally and the combined style-sac and mid-gut leave it postero-ventrally. The mid-gut leaves the right side of the style-sac almost immediately. The minor typhlosole passes forwards a short distance into the stomach. The major typhlosole, accompanied by the intestinal groove, passes forwards into the stomach, curving to the left, and both structures terminate on the anterior floor of the stomach near the opening of the left duct from the digestive diverticula.

The digestive diverticula open into the stomach by two short ciliated ducts, the orifices of which are situated antero-ventrally opposite that of the oesophagus, from which they are separated by a transverse ridge on the anterior floor of the stomach.

The relatively large gastric shield, from which a pointed tooth projects into the lumen of the stomach, covers the roof and left wall of the stomach. A series of three ridges which pass upwards from the right anterior wall on to the roof of the stomach may represent a sorting area.

There is no indication of the presence of a dorsal hood or of a left pouch. The simplicity of the stomach may well be a secondary feature related to the small size of the animal. If this be true, the stomach of *Turtonia* can only be assigned to Stomach Type IV for practical purposes for we have no knowledge

of the features of the ancestral stomach from which that of *Turtonia* may have been derived by simplification.

ERYCINACEA

Erycinidae

Scintilla hanleyi Deshayes. (Fig. 5)

Specimens were obtained on the undersides of coral boulders at low water mark on various small islands in the vicinity of Singapore.

The oesophagus enters by a horizontal slit (O) in the centre of the anterior face of the thin walled, globular stomach. The style-sac (SS) passes obliquely backwards and downwards from the postero-ventral wall of the stomach, and the mid-gut (MG), which is completely separate from it, arises on its right hand side. The major typhlosole (TY) is thick and projects far into the lumen of the mid-gut ; near the mouth of the mid-gut the major typhlosole diminishes and is then joined by a transverse thickening which passes outwards from the mouth of the style-sac. The major typhlosole sweeps forwards, curving gradually to the left, and terminates in a loose spiral of one turn just within the mouth of a deep depression on the left anterior floor of the stomach. The major typhlosole is accompanied in the usual manner by the intestinal groove (IG).

The ducts from the digestive diverticula enter the stomach in two groups. A group of about fifteen such ducts enters the stomach on the left anterior floor and wall, several opening into the above mentioned depression in the mouth of which the major typhlosole terminates, the remainder opening a little higher, on the left anterior wall (DDD^1). The other group of ducts opens on the right anterior wall of the stomach. Here a single large duct opens into the stomach just in front of the intestinal groove and passes directly downwards into the mass of digestive diverticula. In front of this single large orifice, about ten smaller ducts open into a slight hollow which is overhung by a ridge on the right anterior face of the stomach (DDD^2).

Only two sorting areas were found in the stomach. One consists of a small number of irregular folds and grooves on the anterior face of the stomach (SA^7) which pass upwards from the region of the intestinal groove towards the oesophageal orifice. There is also a similar, though smaller, sorting area (SA^6) on the floor of the left pouch (LP).

The dorsal hood (DH) lies on the left anterior stomach wall ; it receives particulate matter from the anterior face of the stomach by means of two ciliated ridges. One of these (R^1) passes upwards and to the left from the above mentioned sorting area (SA^7), while the other ridge (R), which is slightly narrower, passes backwards from the left corner of the oesophageal orifice. Particles are carried out of the dorsal hood by a shallow groove on its left posterior wall.

The left pouch (LP) lies directly below the orifice of the dorsal hood. A series of irregular folds (SA^6) leads upwards into the left pouch from the mouth of the depression in which the major typhlosole terminates, and some of the ducts from the digestive diverticula (DDD^1) open into the stomach above these irregular folds, within the mouth of the left pouch itself.

The gastric shield (GS) is well developed, and covers a large area of the left and posterior walls of the stomach. It invests the mouth of the dorsal hood with a well-developed flare and a rim of the gastric shield borders the dorsal margin of the left pouch. Between the mouths of the dorsal hood and the left pouch, the gastric shield is raised into a conspicuous globular swelling.

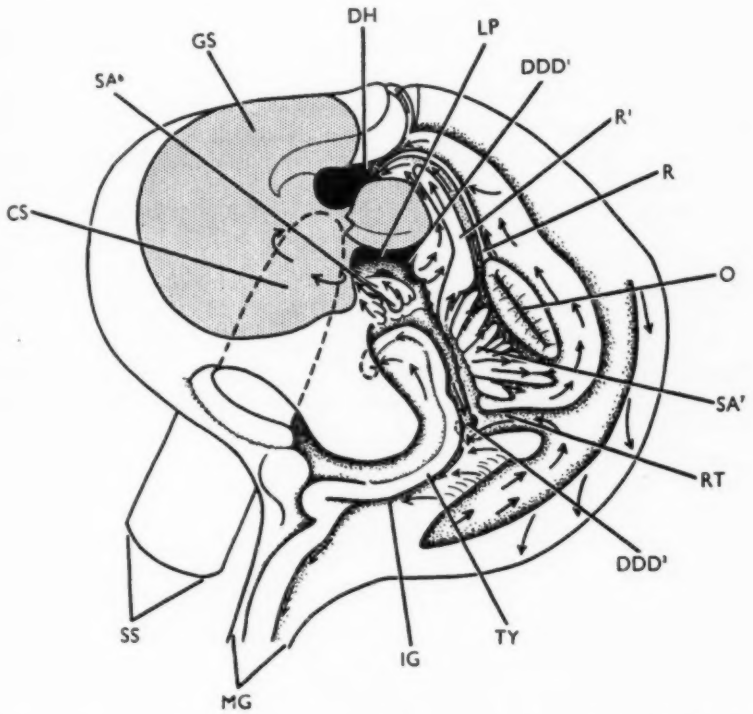


Fig. 5.—*Scintilla hanleyi* Deshayes. Interior of the stomach, seen from the right side, after an incision through its right side extending into the mouth of the mid-gut. × about 20. (For lettering see p. 525).

The crystalline style (CS) projects obliquely forwards and upwards to rest its tip in the mouth of the dorsal hood. In one specimen the style was observed to rotate in a clockwise direction as seen from the anterior end, at the rate of four revolutions in two minutes twenty seconds. In a second specimen of similar size, collected on the same occasion and dissected within a few hours, the style was not revolving.

There is no sorting area within the dorsal hood, nor is there one on the right wall of the stomach. There is a smooth oval depression on the posterior part of the right wall, however, and this may be a relic of the posterior sorting area for it discharges waste material into the intestinal groove via a well defined rejection tract (RT).

Lasaea rubra (Montagu)

Oldfield (1955) has figured and described the interior of the stomach of *L. rubra*. In spite of the very small size of this animal the following facts were elicited. The oesophagus enters the stomach anteriorly ; the style-sac and the mid-gut, which are separate from one another, leave the stomach posteriorly; the major typhlosole, accompanied by the intestinal groove, passes forwards from the mouth of the style-sac across the floor of the stomach and terminates near the orifices of the ducts from the digestive diverticula ; the digestive diverticula open into the stomach by four ducts, the orifices of which lie close together antero-ventrally ; there is a small dorsal pouch (=dorsal hood) anteriorly on the left side of the stomach ; a relatively large gastric shield covers the roof and the left wall of the stomach posteriorly, and it invests the mouth of the dorsal pouch. Oldfield considered that the stomach of *Lasaea* was simplified, with few sorting folds and with a reduced dorsal pouch (=dorsal hood).

Montacutidae

Montacuta ferruginosa (Montagu) (Fig. 6)

The small size of the specimens made it difficult to observe the internal structure of the stomach in any great detail. The following points were ascertained.

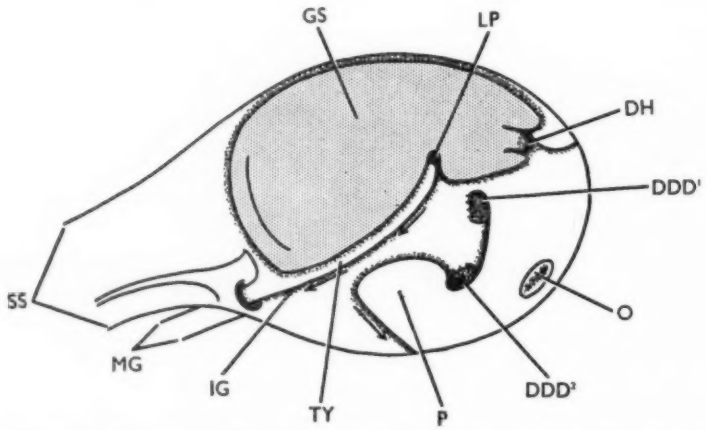


Fig. 6.—*Montacuta ferruginosa* (Montagu). Interior of the stomach, seen from the right side, after opening it by an incision in its right side and extending into the style-sac. × about 40. (For lettering see p. 525).

The stomach is oval in shape, with thin and transparent walls and the oesophagus (O) enters antero-ventrally. The style-sac (SS) is relatively large and stretches backwards horizontally from the posterior end of the stomach. The slender mid-gut (MG) is completely separate from the style-sac, and opens into the stomach a little anterior and ventral to the orifice of the style-sac.

The major typhlosole (TY) emerges from the mid-gut and passes forwards across the floor of the stomach, curving gently towards the left and finally terminating in a slight hollow on the left side of the stomach (LP). Since this hollow is bordered dorsally by the gastric shield (GS), it is possibly the left pouch. It was not possible to determine whether any ducts enter this hollow from the digestive diverticula.

The digestive diverticula open into the stomach via two ducts (DDD^1, DDD^2) the mouths of which lie symmetrically in a shallow hollow on the anterior floor of the stomach. On the right side of the stomach, behind the orifice of the right duct from the digestive diverticula there is a broad raised pad (P). The left side of the stomach is covered by an extensive gastric shield (GS) which bears two small saddle-shaped depressions. One of these lies ventrally and invests the upper border of the left pouch (LP), while the other lies anteriorly on the left side of the stomach and invests the posterior border of a slight hollow which could be interpreted as the dorsal hood (DH).

The major typhlosole is accompanied as usual by an intestinal groove (IG), in which cilia were observed to beat backwards towards the mouth of the mid-gut. No other details of ciliary action could be seen. It is probable that, due to the small size of this genus, some details of structure were missed, such as small ridged sorting areas, but it is also probable that the interior of the stomach of such a small species would exhibit some degree of simplification.

LUCINACEA

Ungulinidae*

Thyasira flexuosa (Montagu) (Fig. 7)

The stomach is small and flimsy, with transparent walls ; the oesophagus (O) enters on its anterior face, and the combined style-sac (SS) and mid-gut leaves horizontally from the posterior end. The minor intestinal typhlosole (MT) terminates on the right side of the floor of the stomach ; the major typhlosole (TY), accompanied by the intestinal groove (IG) passes forwards over the floor of the stomach, bends to the left and terminates on the left anterior floor of the stomach. The digestive diverticula open into the stomach by two wide ducts (DDD) the orifices of which lie on either side of the median line on the anterior floor of the stomach. From each of these apertures one tubule leads upwards, arching over the anterior side of the stomach, and another tubule leads downwards through the relatively small visceral mass and towards the mass of digestive diverticula which project outwards into the mantle cavity on either side of the long slender foot.

On the left side of the stomach there is a small gastric shield (GS), the anterior border of which is saddle-shaped and invests the lower border of a small dorsal hood (DH). The anterior wall of the dorsal hood appears to possess a simple sorting area consisting of three or four folds (SA^3). Two folds (F) arise on the anterior floor of the stomach and pass up the right anterior

* Pelseneer (1906) and Thiele (1934) placed this genus in the family Ungulinidae. In a personal communication, Mr. J. A. Allen states that *Thyasira* should be placed in a separate family, the Thyasiridae.

wall of the stomach towards the region of the dorsal hood. There was no indication of a left pouch.

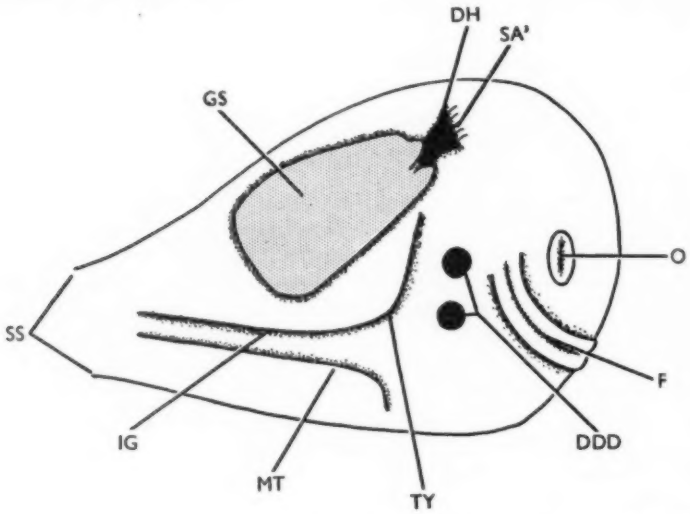


Fig. 7.—*Thyasira flexuosa* (Montagu). View of the interior of the stomach, seen from the right side, after a mid-dorsal incision through the roof and extending into the style-sac. Diagrammatic. (For lettering see p. 525).

Lucinidae

Lucinoma (*Phacoides*) *borealis* (L.) (Fig. 8)

The specimens studied were relatively small and the tissues were rather transparent, making it difficult to study the interior of the stomach in any great detail.

The long and slender oesophagus (O) enters the antero-ventral surface of the elliptical stomach. The combined style-sac (SS) and mid-gut leave the posterior wall of the stomach. The minor typhlosole (MT) terminates on the right wall of the stomach, close to the orifice of the mid-gut. The major typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards over the floor of the stomach, curving sharply to the left and terminating in a hollow on the left side of the stomach into which open two or three ducts from the digestive diverticula (DDD^1). This cavity might possibly be interpreted as a left pouch.

A second group of three ducts from the digestive diverticula open separately into the stomach high up on its right side (DDD^2).

The gastric shield (GS) is relatively small and flimsy. It lies on the left side of the stomach, above the hollow (DDD^1) into which open the ducts from the digestive diverticula of the left side. The gastric shield does not invest the mouth of this hollow. Anteriorly the gastric shield bears a saddle-shaped depression which fits into the mouth of a depression which may be interpreted

as the dorsal hood (DH). The walls of the dorsal hood, and the anterior and right sides of the stomach appear to be devoid of sorting areas.

The few ciliary currents which could be detected in such small specimens are depicted in the figure.

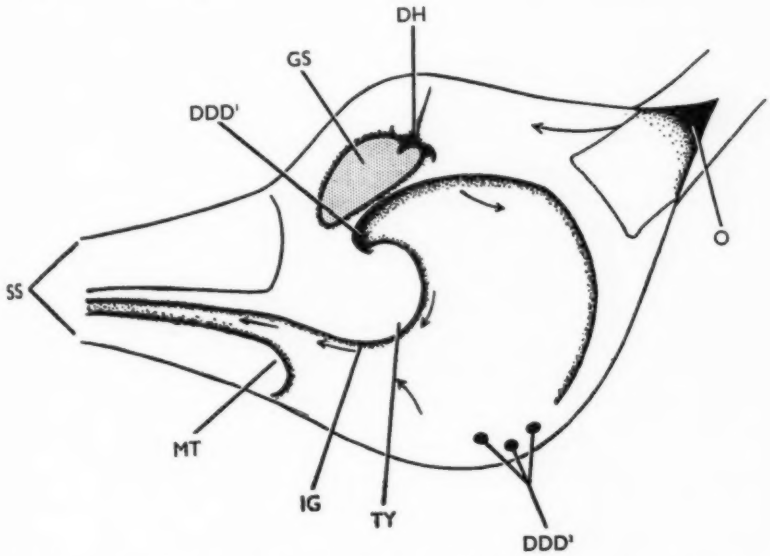


Fig. 8.—*Lucinoma* (*Phacoides*) *borealis* (L.). View of the interior of the stomach after a mid-dorsal incision extending from the oesophagus into the style-sac. × about 30. (For lettering see p. 525).

The stomach of *Lucinoma* seems to be unusually simple in form. The ducts of the digestive diverticula are also unusual in their small number, their simplicity, and in their appearance—the three main ducts on each side of the stomach are relatively long and slightly branched, and their walls are covered with dark specks as though their lumina contained small and very dark granules.

CHAMACEA

Chamidae

Chama multisquamosa Reeve (Fig. 9)

The slender oesophagus (O) enters an anterior hemispheric "vestibule" (V) which is separated from the main chamber of the stomach by a conspicuous ventral rim (RV). Slow ciliary currents carry material over the walls of this antechamber towards the anterior side of this rim where a ciliated tract conveys material transversely to the left, round the margin of the gastric shield (GS) and into the dorsal hood (DH). Posterior to this rim there is a small sorting area (SA^7) on which cilia beat anteriorly.

The combined style-sac (SS) and mid-gut leave the posterior wall of the stomach. The minor typhlosole (MT) terminates on the right posterior wall

of the stomach, close to the orifice of the mid-gut. The major typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards on to the floor of the stomach, curving in a wide semicircle to the left. Both structures ultimately enter a deep aperture on the left anterior floor of the stomach, into which open numerous ducts from the digestive diverticula ; both structures pass vertically downwards and penetrate to the apex of this pocket.

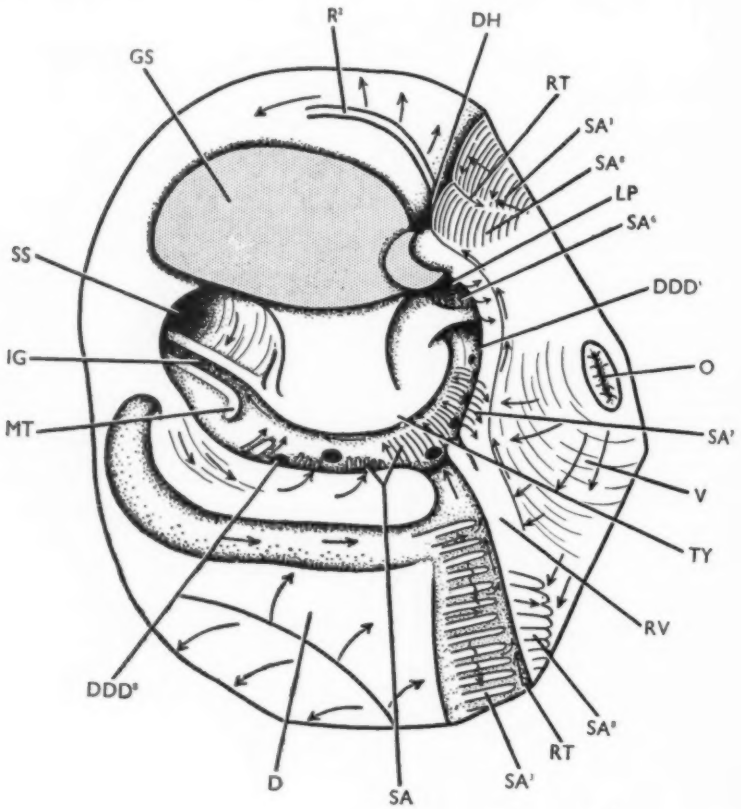


Fig. 9.—*Chama multisquamosa* Reeve. View of the interior of the stomach, seen from the right side, after opening by a horizontal incision in the right side. (For lettering see p. 525).

About eight ducts from the digestive diverticula (DDD¹, DDD⁸) open directly into the stomach, their orifices being spread out in a series at a little distance from the intestinal groove (IG). A sorting area (SA) of fine ridges and grooves lies between the orifices of these ducts from the digestive diverticula and the intestinal groove. Cilia in the grooves of this sorting area direct particles along the grooves towards and into the intestinal groove. The posteriormost of the ducts in this series (DDD⁸) lies on the right posterior wall of the stomach close to the mouth of the mid-gut, from which it is separated

by a finger-like ridge which projects at right angles towards the intestinal groove. This finger-like ridge is the posteriormost and largest ridge of the sorting area mentioned above (SA).

The dorsal hood (DH) lies antero-dorsally on the left side of the stomach. The smooth posterior wall bears a ridge (R^2) ; its anterior wall bears two sorting areas which are separated by a ciliated rejection tract (RT). The uppermost sorting area (SA^3) consists of transverse ridges and grooves and extends over the roof of the stomach and down its right side. Cilia on the crests of the ridges beat transversely over the crests and towards the apex of the dorsal hood. Cilia in the grooves beat along the grooves and into the ciliated rejection tract (RT). The rejection tract discharges waste material into the intestinal groove (IG). The part of this sorting area which lies on the right wall of the stomach consists of ridges which are well spaced out. Posterior to this sorting area there is a wide triangular area (D) on the right side of the stomach, over which cilia beat forwards and downwards, discharging waste material into the end part of the rejection tract. A conspicuous elevation passes forwards from the right border of the mouth of the mid-gut, separating this area (D) from the posterior part of the sorting area (SA) and from the series of orifices of ducts from the digestive diverticula. The second sorting area in the dorsal hood (SA^8) passes over the roof of the stomach and ends on the right side, anterior to the rejection tract (RT).

There is a small left pouch (LP) on the left anterior wall of the stomach, below the mouth of the dorsal hood. The floor of this pouch bears a small sorting area (SA^6). A number of small ducts from the digestive diverticula opens into the left pouch. The gastric shield (GS), which is relatively small, invests the mouth of the dorsal hood and also sends a small flare over the posterior rim of the left pouch.

SAXICAVACEA

Saxicavidae

Hiatella arctica L. (Fig. 10)

The stomach is globular in shape ; the oesophagus (O) enters the stomach anteriorly and the combined style-sac (SS) and mid-gut leave it postero-ventrally. The minor typhlosole (MT) terminates in the mouth of the mid-gut, while the major typhlosole (TY) passes forwards over the floor of the stomach until it reaches the anterior end, when it turns sharply to the left. The major typhlosole curves in an incomplete spiral and terminates on the median side of a pocket (DDD^1) in the left anterior floor of the stomach. About six ducts from the digestive diverticula open into this pocket. The major typhlosole is accompanied throughout its course by the intestinal groove (IG).

The dorsal hood (DH) is moderately well developed and lies high on the left side of the stomach. The posterior wall of the dorsal hood bears two longitudinal ridges (R^2) between which a rejection current is situated. The anterior wall of the dorsal hood bears a sorting area (SA^8) of ridges and grooves on which cilia beat downwards towards a longitudinal ridge (R). The sorting

area and the accompanying ridge pass backwards from the left corner of the oesophageal orifice into the dorsal hood.

The left pouch (LP) is a shallow pocket which lies anterior and ventral to the mouth of the dorsal hood. Three ducts enter the left pouch from the digestive diverticula. A sorting area (SA^7) of vertical folds lies on the anterior face of the stomach, between the orifice of the oesophagus and the intestinal groove. This sorting area extends on to the left anterior wall of the stomach,

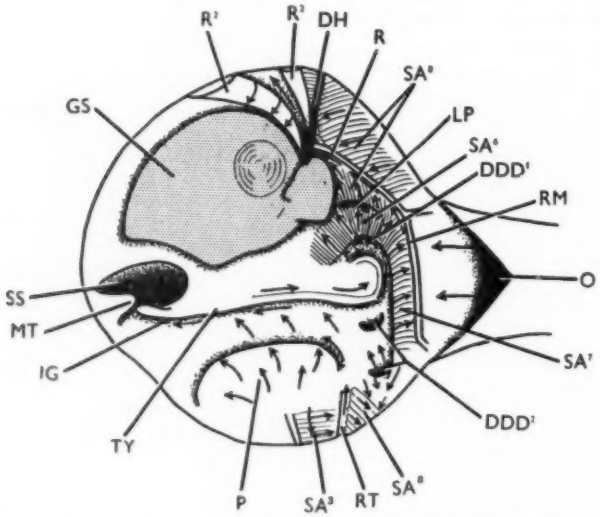


Fig. 10.—*Hiatella arctica* L. View of the interior of the stomach after opening by a mid-dorsal incision. (For lettering see p. 525).

invades the left pouch (SA^6), and reaches up to the above mentioned longitudinal ridge (SA^8). Ciliary currents on this sorting area are directed along the grooves towards the longitudinal ridge (R). Along this ridge cilia direct particles backwards, over the anterior face of the dorsal hood and into the dorsal hood.

The posterior part of the left wall of the stomach is covered by an extensive and well developed gastric shield (GS), in the centre of which there is a hemispheric prominence. The gastric shield invests the mouth of the dorsal hood with a saddle-shaped lobe, and the anteriormost part of the gastric shield just reaches and invests the posterior rim of the left pouch.

As mentioned above, the digestive diverticula on the left side open by nine ducts, three of which enter via the left pouch. The digestive diverticula on the right side open by two ducts (DDD^2), a large one opening on the anterior floor close to the point where the major typhlosole turns sharply to the left, and a slightly smaller one a little higher on the right anterior wall.

On the right side of the stomach, immediately dorsal to the intestinal groove (IG) there is a raised pad (P) on which conspicuously long cilia beat downwards towards the intestinal groove. Dorsal to this pad there is a

sorting area bordered on its anterior side by a rejection tract (RT) which discharges particles from the dorsal hood into the intestinal groove. Cilia on the crests of the folds of this sorting area beat transversely over the crests and towards the dorsal hood, while the cilia in the grooves between the folds beat along the grooves and into the above mentioned rejection tract.

GASTROCHAENACEA

Gastrochaenidae

Rocellaria cuneiformis Spengler

The stomach of *R. cuneiformis* has been figured and described by Purchon (1954), and further specimens have also been examined. The following main features have been noted : The oesophagus enters the stomach anteriorly ; the combined style-sac and mid-gut leaves the stomach postero-ventrally ; the minor typhlosole—previously wrongly labelled (Fig. 11, TY, Purchon, 1954)—terminates on the right side of the stomach close to the orifice of the mid-gut. The major typhlosole, accompanied by the intestinal groove, passes forwards over the floor of the stomach curving gradually to the left, and terminates in an orifice on the left anterior wall of the stomach. Purchon (1954) called this cavity the " left caecum ", but the writer now questions whether this term is appropriate for descriptions of stomachs of Type IV. A group of about nine ducts from the digestive diverticula open into the stomach on its left anterior wall, the majority opening into the above mentioned orifice in which the major typhlosole terminates, while the remainder open on the left wall just above this orifice. A second group of ducts from the digestive diverticula opens on the right anterior wall via one large and one small orifice.

There is a well developed dorsal hood on the left wall of the stomach anteriorly, and it bears a sorting area (SA^3) on its roof ; there is a left pouch below the mouth of the dorsal hood, and apparently a single duct enters the left pouch from the digestive diverticula. There is a gastric shield which invests the mouth of the dorsal hood and also that of the left pouch. There is a sorting area of fine ridges and folds on the anterior face of the stomach, somewhat more extensive than originally indicated by Purchon (1954). This sorting area is very similar in extent to that described above for *Hiatella arctica* (see above). The sorting area extends below the orifice of the oesophagus across to the ducts from the digestive diverticula on the right side ($=SA^7$), it extends to the left into the left pouch ($=SA^6$), it extends upwards on the left to the ridge which leads back to the dorsal hood ($=SA^8$).

PANDORACEA

Pandoridae

Pandora inaequivalis L. (Fig. 11)

The interior of the stomach of *P. inaequivalvis* has been figured and described by Allen (1954), and comparison of his figure with that given here will show a general agreement as to the general structure of the stomach. The present writer cannot wholly agree with the interpretations offered by Allen,

however, and it has been considered necessary to provide a fresh description and illustration in order to gain consistency in the use of technical terms. Much of the difficulty in interpretation arises from the presence of a single duct from the digestive diverticula (DDD^3) which Allen (1954) established as entering the middle of the floor of the stomach, and which he erroneously interpreted as the "right caecum". This duct communicates with the intestinal groove (IG) by a shallow groove (G). The present writer did not have access to the above mentioned paper by Allen when studying *P. inaequivalvis* and did not observe this structure, which must certainly have been relatively smaller than that depicted in Allen's figure. The orifice of this duct (DDD^3) and the shallow groove approaching it have been inserted in Fig. 11, the orifice of the duct being deliberately shown somewhat smaller than in Allen's figure. The failure of the present writer to detect the presence of this duct may be attributed to the small size of the specimens studied and the view of underlying structures through the thin and transparent stomach wall.

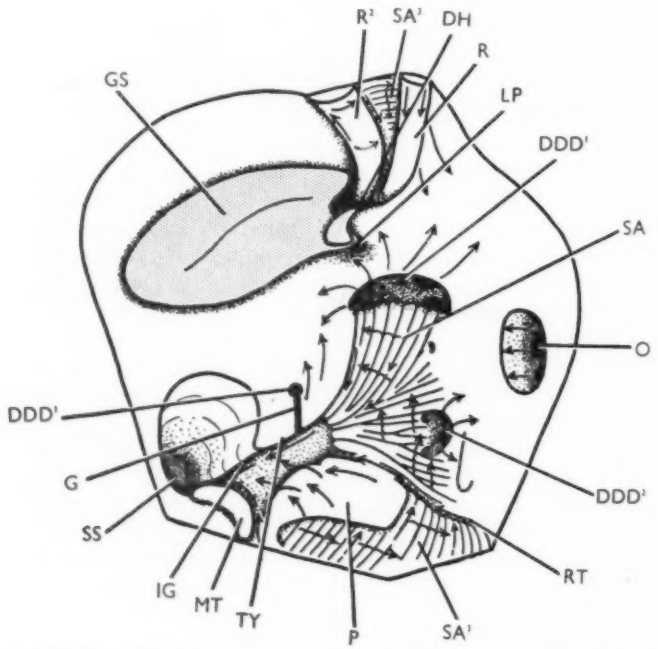


Fig. 11.—*Pandora inaequivalvis* L. The interior of the stomach, seen from the right side, after opening by making an incision in the right wall. (For lettering see p. 525).

The short oesophagus (O) enters the anterior face of the stomach by an oval aperture, while the combined style-sac (SS) and mid-gut leave the stomach postero-ventrally. The minor typhlosole (MT) curves forwards from the mouth of the mid-gut and terminates low down on the right posterior wall of the stomach. The major typhlosole (TY), accompanied by the intestinal

groove (IG), passes forwards on to the floor of the stomach. Allen (1954) considered that the two structures curved abruptly to the left and passed into the above mentioned duct (DDD^3) from the digestive diverticula. The present writer, overlooking that duct, originally considered that the major typhlosole and intestinal groove passed further forwards to terminate at the posterior border of a far larger orifice (DDD^1) on the left anterior wall of the stomach and, on the whole, is still inclined to that view.

The dorsal hood (DH) leaves the stomach dorsally and curves forwards and to the left. Ridges on the anterior and posterior walls (R, R^2) of the dorsal hood subtend a sorting area (SA^3) of horizontal ridges and grooves, which extends over the roof of the stomach and down its right side. This sorting area extends backwards towards the end of the minor typhlosole (MT), there being a raised ciliated pad (P) between the posterior part of the sorting area (SA^3) and the intestinal groove (IG). Cilia on the crests of the folds beat transversely over the crests and towards the apex of the dorsal hood, while cilia in the grooves beat along the grooves and into a rejection tract (RT) which discharges into the intestinal groove (IG).

A well developed gastric shield (GS) lies on the left wall of the stomach and invests the mouth of the dorsal hood with a small flare. Immediately below the mouth of the dorsal hood there is a small blind hollow into which the anterior border of the gastric shield fits. This hollow is considered to be the left pouch (LP). Allen implied by his choice of words that a duct or ducts from the digestive diverticula open into the left pouch, but it was concluded in the present study that this was not so.

On the anterior floor of the stomach there is a fanshaped sorting area (SA) of ridges and grooves which radiate forwards and outwards from the intestinal groove. Allen (1954) described this area as " lateral rejection grooves " and considered that they served in place of the intestinal groove as an organ of rejection. The present writer cannot accept these views. This sorting area penetrates two large apertures, one on the left anterior wall (DDD^1) into which open four ducts from the digestive diverticula, and outside which a fifth duct opens, and the other on the right anterior wall (DDD^2) into which open all the ducts from the digestive diverticula on the right side of the stomach. The aperture on the left anterior wall of the stomach was termed the " left caecum " by Allen (1954), but the present writer questions whether this term is appropriate for descriptions of stomachs of Type IV. Cilia on the crests of the folds of this sorting area (SA) beat transversely over the crests from right to left, those on the extreme right conveying particles into the mouth of the ducts from the digestive diverticula on the right side (DDD^2). This is not considered to constitute an acceptance tract, for such material is immediately driven out of the mouth of the duct and passed further to the left. Cilia in the grooves of this sorting area beat along the grooves and convey waste material into the intestinal groove.

Allen (1954) noted the presence of a groove on the roof of the stomach, in which cilia beat backwards and convey particles from the orifice of the oesophagus towards and into the dorsal hood.

Allen (1954) suggested that the differences between the stomach of *Pandora* and those of other Lamellibranchia are a possible consequence of elongation. He evidently did not recognise the similarity between the stomachs of *Pandora* and of *Anodonta* (Graham, 1949), nor could he have been aware that this type of stomach is to be found in some twenty families of Filibranchia and Eulamellibranchia as described in this paper. This particular form of stomach is not the consequence of the adoption of certain habitats or growth forms, but is probably the expression of a certain phylogeny of Lamellibranchia. The writer is particularly grateful to Mr J. A. Allen for a personal communication which was of great assistance in trying to interpret the internal structure of the stomach of *Pandora*.

Laternulidae

Laternula rostrata Sowerby (Fig. 12)

Specimens were obtained from stiff intertidal muds on the seaward margin of mangrove swamps on the north coast of Singapore island, in the Straits of Johore.

The stomach is thin-walled, and is globular in shape with a conical forward projection into which the oesophagus (O) opens. The combined style-sac (SS) and mid-gut passes directly downwards from the posterior and ventral wall of the stomach. The major typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards from the mouth of the mid-gut and curves to the left in a semi-circle over the floor of the stomach. It terminates on the median side of an orifice on the left anterior floor of the stomach into which open three ducts from the digestive diverticula (DDD^1). The digestive diverticula of the right side of the body open into the stomach by one large duct (DDD^2) which lies on the right anterior wall of the stomach.

There is a very well developed dorsal hood (DH) which arises from the roof of the stomach and curves over towards the left side. There are two sorting areas, separated from one another by a rejection tract (RT), on the roof of the dorsal hood. Particles entering the stomach from the oesophagus will fall on a wide smooth expanse over which ciliary currents beat upwards, conveying particulate material to the rim (RM) which surrounds the oesophageal orifice. Here transverse ciliary currents direct material to a longitudinal ridge (R) on the roof of the stomach, and backwards along this ridge into the dorsal hood. On the left anterior stomach wall strong ciliary currents direct particles towards this longitudinal ridge. Thus all material entering the stomach is conveyed in the first instance to the dorsal hood. Ciliary sorting mechanisms within the dorsal hood ensure that material is circulated here for some time. Thus on the posterior of the two sorting areas (SA^3) strong ciliary currents pass over the crests of the folds, and carry particles towards the apex of the dorsal hood, while ciliary currents in the grooves between the folds carry particles towards and into the rejection tract (RT). If much material is present it tends to be passed from the rejection tract on to the anterior sorting area (SA^8) by which the mucus-bound material is carried forward to join the incoming material alongside the ridge (R) on the anterior face of the dorsal

hood and so passes back into the depths of the dorsal hood. Waste material from the dorsal hood is discharged via the rejection tract (RT), which passes over the roof and down the right side of the stomach, into the intestinal groove (IG).

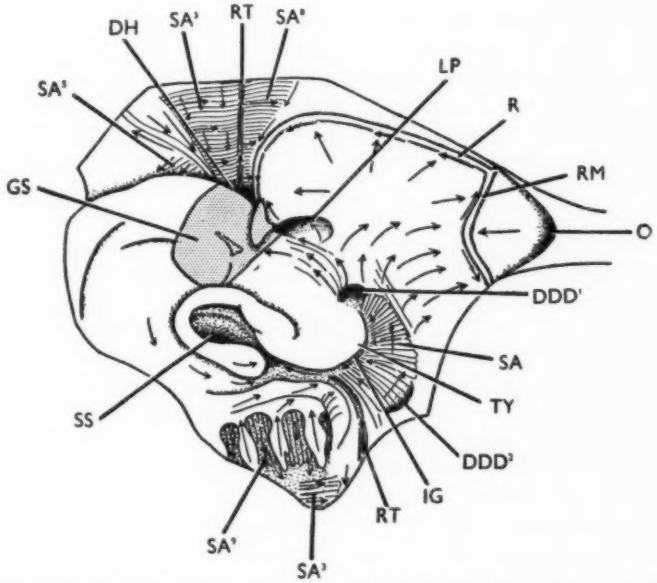


Fig. 12.—*Laternula rostrata* Sowerby. View of the interior of the stomach, seen from the right side, after opening by an incision in the right side. × 9. (For lettering see p. 525).

There is a small, but well-defined left pouch (LP) on the left anterior wall of the stomach, antero-ventral to the mouth of the dorsal hood. No ducts enter the left pouch from the digestive diverticula. There is a small gastric shield (GS), which sends a lobe into the mouth of the dorsal hood and which also invests the posterior corner of the mouth of the left pouch.

On the anterior face of the stomach there is a sorting area (SA) which extends between the two ducts from the digestive diverticula (DDD^1, DDD^2) into each of which the sorting area penetrates. Ciliary currents on the crests of the folds pass transversely to the left and so carry particles into the left duct from the digestive diverticula (DDD^1), while cilia in the grooves discharge material into the intestinal groove (IG). Material is carried away from the left duct from the digestive diverticula either over its left and posterior border into the left pouch and thence doubtless to the dorsal hood, or via the intestinal groove to the mid-gut.

There is a further sorting area (SA^3) on the right posterior wall of the stomach. As seen by transparency in an undissected stomach this sorting area is semi-circular and it consists of a number of large elevated tongues which are separated from each other by areas of narrow ridges and grooves. The tongues and the ridges between them are arranged radially and focus

on a point high on the right side of the stomach and close to the mouth of the dorsal hood. Ciliary currents on the tongues pass waste material downwards towards the intestinal groove, while the ciliary currents on the areas of fine ridges and grooves collect material and pass it upwards and into the dorsal hood.

When freshly opened, the contents of the stomach are usually found to be glutinous, and sticky threads pass into the dorsal hood and into the two ducts serving the digestive diverticula. It is probable, therefore, that food material is not passed into the system of digestive diverticula as isolated particles in suspension, but is dragged in, in the form of continuous threads, by ciliary action. It is possible that by the time the food material has reached the digestive tubules these sticky threads will have liquefied, due to a change in pH.

Cochlodesma praetenue (Pulteney)

An illustrated account of the interior of the stomach of *C. praetenue* has recently been given by Allen (1958) who refers therein to a personal communication from Purchon. It must be emphasised that the communication in question referred to *Pandora*, not to *Cochlodesma*—which the present writer has not yet studied—and that the entry in the above-mentioned paper gives a misleading and incomplete impression of Purchon's views.

The present paper treats with the stomach of four members of the Anomalodesmata, namely *Pandora*, *Laternula*, *Cleidothearus* and *Myadora* (Figs. 11–14). It can readily be seen, from inspection of these figures, that although there is much in common, yet there is a considerable degree of variation in stomach structure in the Anomalodesmata. The stomach of *Cochlodesma* is generally comparable with these examples, but differs from each in one or more respects. It is the considered view of the present writer that certain features of the stomach of *Cochlodesma* have been mid-identified by Allen (1958) and the following interpretation is therefore offered, to bring the records for *Cochlodesma*, into line with the present review. In the following references to the stomach of *Cochlodesma* the labels are those of Fig. 8 in Allen (1958).

The left pouch (LP) of *Cochlodesma* is directly comparable with the left pouch, similarly labelled, in the present paper. The ducts from the digestive diverticula opening on the left anterior floor of the stomach of *Cochlodesma* (LD) correspond with those opening just outside the left pouch in *Myadora* (Fig. 14, DDD^2) or just inside the left pouch in *Cleidothearus* (Fig. 13, LP). The group of three orifices by which ducts open on the median and right anterior floor of the stomach of *Cochlodesma* (RD) correspond with the two similarly placed orifices in *Myadora* (Fig. 14, DDD^3) and in *Cleidothearus* (Fig. 13, DDD^2, DDD^3). The ducts which enter the left posterior floor of the stomach of *Cochlodesma* (C) by an orifice described as " probably the right caecum ", undoubtedly corresponds with the similarly placed orifice in *Cleidothearus* and in *Myadora* (Figs. 13 and 14, DDD^1). Comparisons with *Pandora* and *Laternula* have been omitted for in some cases—but not all—the comparisons are less certain. There can be no doubt that this posteriormost orifice in *Cochlodesma*, where the major typhlosole terminates, cannot possibly be a " right caecum ", of which it possesses *none* of the essential attributes (Purchon, 1955).

The system of ridges and grooves on the anterior floor of the stomach of *Cochlodesma* (LRG), described by Allen as "lateral rejection grooves", is clearly comparable with the anterior sorting area (SA) as described in the present paper for many examples. Allen considered that this system of ridges and grooves replace the intestinal groove, in *Pandora* and in *Cochlodesma*. The present writer can find no grounds for supporting this view.

Chamostreidae

Cleidothearus albidus Lam. (Fig. 13)

The long and slender oesophagus passes obliquely backwards and upwards. Its interior is longitudinally ridged, and the point at which it opens into the stomach (O) is marked by a transverse ridge. The anterior part of the stomach, into which the oesophagus opens, might be termed a vestibule (V) for there is here a distinct chamber which leads backwards into the much larger main part of the stomach.

The style sac (SS) and mid-gut, which are conjoined, pass vertically downwards from the posterior floor of the stomach. The minor intestinal typhlosole (MT) is a broad flat band which terminates on the right side of the stomach close to the mouth of the mid-gut. The major typhlosole (TY) does not extend far forwards over the floor of the stomach as is customary, but bends sharply to the left as soon as it enters the stomach and terminates just posterior and external to a large orifice (DDD^1) which receives about six ducts from the digestive diverticula on the left side of the stomach. The intestinal groove (IG) accompanies the major typhlosole.

There is a well developed gastric shield (GS) on the left side of the stomach. Dorsally a very deep saddle-shaped flare of the gastric shield enters the dorsal hood (DH) and invests its lower border, while antero-dorsally the gastric shield invests the mouth of the left pouch (LP). The left pouch is a moderately deep hemispheric pocket which receives one small duct from the digestive diverticula.

The remainder of the digestive diverticula open into the stomach via two large orifices which lie close together on the floor of the stomach near the median line. About six ducts open into the left of these orifices (DDD^2), while three ducts open into the other (DDD^3).

The dorsal hood (DH) is capacious and its walls bear extensive sorting areas. A ridge (R) passes backwards from the right corner of the opening of the oesophagus into the stomach, over the roof of the stomach and into the dorsal hood low down on its anterior side. This ridge is bordered on each side by folded sorting areas (SA^8) over which cilia beat along the grooves and towards the ridge (R). Ciliary currents beat along the sides of the ridge (R) towards and into the dorsal hood. A more slender ridge emerges from the dorsal hood on its posterior wall (R^2), and ventral to this the posterior wall of the dorsal hood bears a very fine sorting area (SA^5) on which cilia beat downwards and convey particles out of the dorsal hood. Yet a fourth sorting area is found on the roof of the dorsal hood (SA^3); here cilia on the crests of the folds beat transversely over the folds and deeper into the dorsal hood, while

cilia in the grooves between the folds beat along the grooves anteriorly, and discharge material down the right side of the stomach, posterior to the right hand duct (DDD^3) from the digestive diverticula.

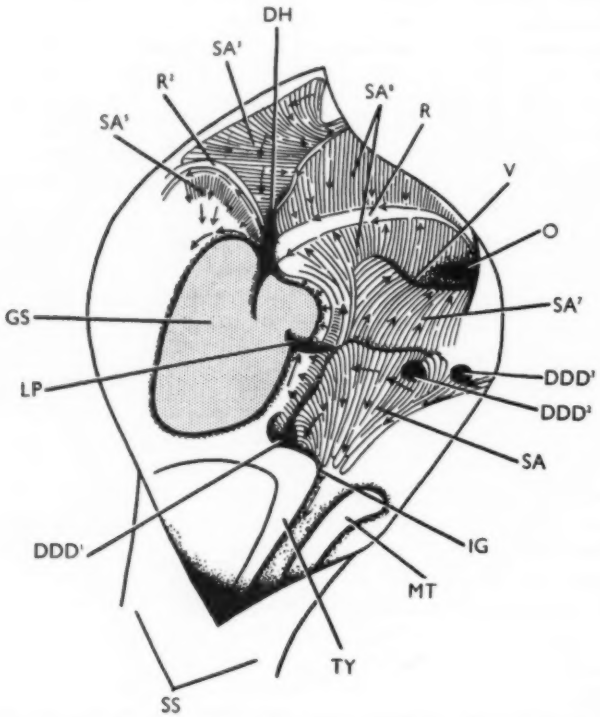


Fig. 13.—*Cleidothearus albidus* Lam. Interior of the stomach, seen from the right side, after an oblique incision in the right wall running from the oesophagus to the style-sac. × about 8. (For lettering see p. 525).

There is a sorting area (SA^7) of parallel ridges and grooves which lies on the anterior floor of the stomach, passes into the vestibule (V), and penetrates to the lower border of the orifice of the oesophagus. On this sorting area ciliary currents are directed anteriorly along the folds. Consequently all material entering the stomach from the oesophagus is necessarily passed first towards the dorsal hood via the two sorting areas (SA^8) and the ridge (R) lying on the roof of the stomach.

There is yet one more sorting area on the posterior floor of the stomach. Its ridges and grooves arise at the posterior border of the sorting area (SA^7) just mentioned above, and they penetrate the left pouch (LP) and the three orifices (DDD^1, DDD^2, DDD^3) into which open the ducts from the digestive diverticula. The folds of this sorting area (SA) are directed backwards and converge on the intestinal groove and the mouth of the mid-gut. Cilia on the crests of the folds beat transversely from right to left ; cilia in the grooves

beat along the grooves towards the intestinal groove. This sorting area is joined by five or six ridges which discharge waste material from the sorting area (SA^3) on the roof of the dorsal hood, and which pass posterior to the right duct from the digestive diverticula (DDD^3) as mentioned above. Within the mouths of the two anterior ducts from the digestive diverticula the ciliary currents on the folds cause particles to pass from right to left and gradually backwards out of the ducts and into the stomach.

The most striking feature of the interior of the stomach of *Cleidothearus* is the large number of sorting areas, and their great development. Two alternative explanations for this remarkable development of sorting areas may be considered. First, that the genus inhabits waters in which much suspended material is present, that the ciliary sorting mechanisms of the ctenidia and labial palps are inadequate, and that much sorting and rejection of waste material has to be effected in the stomach ; second, that for some reason it is necessary to protract the period of circulation of particulate food material in the lumen of the stomach. The writer prefers the second alternative, for the greater part of the sorting areas in the stomach appear to be concerned with circulation rather than with sorting and rejection.

Myochamidae

Myadora ovata Reeve (Fig. 14)

The following account and the accompanying illustration are derived from a personal communication from Mr G. Owen, who obtained specimens of *M. ovata* at Menzies Bay, Banks Peninsula, New Zealand.

The globular stomach is surrounded by greenish digestive diverticula ; the oesophagus (O) enters anteriorly and the combined style-sac (SS) and mid-gut leave the stomach postero-ventrally. The digestive diverticula on the right side of the stomach open by two ducts (DDD^3), a large one ventral to the oesophageal orifice and a smaller one on the right side of the stomach. The major typhlosole (TY) emerges from the combined style-sac and mid-gut and turns slightly to the right over the floor of the stomach. It then bends sharply to the left and terminates on the left floor of the stomach at the mouth of a deep embayment (DDD^1) into which open a number of ducts from the digestive diverticula on the left side. The major typhlosole is accompanied as usual by the intestinal groove (IG).

The well-developed dorsal hood (DH) opens on the left side and roof of the stomach, its mouth being invested by a large saddle-shaped flare of the gastric shield (GS). The dorsal hood passes forwards as a blind tubular projection along the left side of the stomach. The left pouch (LP) lies antero-ventral to the mouth of the dorsal hood, the posterior border of its mouth being protected by a flare of the gastric shield. At least two ducts from the digestive diverticula (DDD^2) enter the left pouch. The gastric shield covers a large area on the left and posterior sides of the stomach. It possesses a prominent tooth at the mouth of the dorsal hood (T).

The sorting area on the anterior floor of the stomach (SA) is well developed. It extends into the mouth of the left pouch (LP) and into the mouths of the

ducts from the digestive diverticula on the left (DDD^1) and right (DDD^3) sides of the stomach. Ciliary currents on this sorting area direct particles from the right to left over the crests of the folds, while in the grooves between the folds the ciliary currents pass waste material into the intestinal groove in which ciliary currents pass backwards, as usual, to the mid-gut.

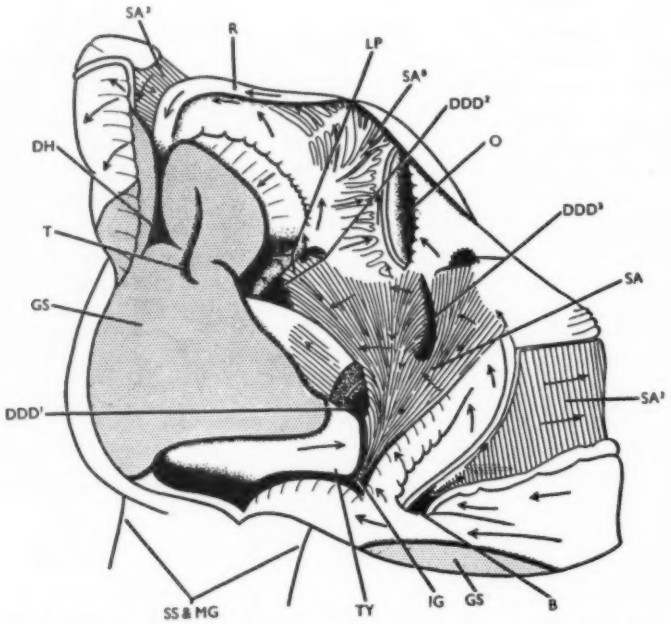


Fig. 14.—*Myadora ovata* Reeve. The interior of the stomach, seen from the right side, after an incision in the right wall from the oesophagus to the style-sac. × 22. From the original by Mr. G. Owen. (For lettering see p. 525).

There is a sorting area of transverse ridges and grooves (SA^3) on the roof of the dorsal hood. This sorting area extends far over the right side of the stomach and into a blind pocket (B) posteriorly. Ciliary currents direct particles transversely over the crests of the ridges of this sorting area and into the dorsal hood. Within the dorsal hood cilia in the grooves between the folds beat anteriorly along the grooves towards a ridge (R) which enters the dorsal hood and along which cilia beat inwards. It was not possible, however, to detect ciliary currents along the grooves in the region of the sorting area on the right wall of the stomach, nor was it possible to detect a rejection tract which one would expect to find along its anterior border, passing waste material down to the intestinal groove.

There is an irregular sorting area (SA^8) on the roof of the stomach, which collects particulate material and directs it backwards along a conspicuous ridge (R) into the dorsal hood.

CLAVAGELLACEA

Clavagellidae

Brechites penis (L.)

In the spring of 1954 the writer found a single living specimen of *B. penis* on the S.E. coast of the island of Singapore, and as much as possible was learned of the ciliary cleansing and feeding mechanisms (Purchon, 1956 a). It was not possible also to make a study of the interior of the stomach while the animal was still alive. Subsequently, however, the preserved animal was dissected, and the following data regarding the internal structure of the stomach were ascertained :—

The style-sac and mid-gut are conjoined and leave the stomach antero-ventrally. The dorsal hood occupies a typical position and possesses a sorting area which extends some distance on to the right side of the stomach. A left pouch is present, but it was not possible to decide whether any ducts open into it from the digestive diverticula. The gastric shield is typical, and invests the mouth of the dorsal hood and also that of the left pouch with flares. The digestive diverticula open into the stomach by a pair of relatively large apertures lying symmetrically on the antero-ventral wall, and by a single aperture lying postero-dorsally on the right wall of the stomach. An extensive sorting area of ridges and grooves lies on the anterior floor of the stomach. The major typhlosole is inconspicuous ; it does not enter the orifices by which the digestive diverticula communicate with the stomach.

DISCUSSION

Purchon (1957) defined Stomach Type IV as found in the Trigoniidae, Limidae, Pectinidae and Anomiidae, and observed that stomachs of somewhat similar internal structure had been recorded in various families in the Eulamellibranchia. No significant differences have been found between the stomachs of the four families mentioned above and those described in the present paper, and all are accordingly assigned to Stomach Type IV. In reaching this conclusion, each feature of the stomach has been examined in turn, the outstanding points being as follows.

1. *The relation between the style-sac and the mid-gut.* The style-sac and mid-gut are conjoined and leave the posterior or postero-ventral wall of the stomach in the majority of cases. The style-sac and mid-gut are wholly separate in the Anomiidae, Erycinidae and Montacutidae, and almost completely separate in the Cyamiidae. It is probable that the condition in the Erycinidae and Montacutidae derives from their common ancestry, but the comparable condition probably arose independently in the Anomiidae. In these families the minor typhlosole is absent.

2. *Termination of the major typhlosole and intestinal groove.* These structures pass forwards over the floor of the stomach, curving gradually or more abruptly to the left. In the Pectinidae, Limidae and in *Anomia* in the Anomiidae they terminate in the broad depression termed the left pouch (Purchon, 1957), as also in the Montacutidae. In *Placuna* in the Anomiidae,

however, their termination is a little distant from the depression which is bordered by the gastric shield, and lies close to the orifices of the ducts from the digestive diverticula of the left side of the body (Purchon, 1957). In the Trigoniidae (Purchon, 1957), and in the majority of cases here described, they terminate at a little distance from the left pouch, and in close association with the orifices of ducts from the digestive diverticula on the left side. Undoubtedly the significant feature is the relationship between the intestinal groove and the orifices of certain of these ducts, and it is probably just a matter of chance that in certain cases these orifices are situated very close to the gastric shield. In the Unionidae, Chamidae and Gastrochaenidae the major typhlosole and intestinal groove do not end on the floor of the stomach, but penetrate to the apex of a deep chamber into which open numerous ducts from the digestive diverticula on the left side. Here again there is no essential difference in form, for all that has happened is that the left anterior floor of the stomach has become deeply embayed.

In the Carditidae the major typhlosole and the accompanying intestinal groove end in a tight spiral on the left anterior floor of the stomach. In all cases these structures curve to the left, and in some cases there is a distinct hint of spiral structure e.g. in the Astartidae (Fig. 2), Erycinidae (Fig. 5) and Lucinidae (Fig. 8). It is considered that this spiral form has been exaggerated in the Carditidae, forming a particularly effective mechanism for the rejection of unwanted material. Owing to the small size of the specimens, the precise conditions in the Ungulinidae were not determined, but there are no grounds for considering them to be other than typical.

3. *The relationship between the gastric shield and the left pouch.* In most cases the gastric shield extends into the left pouch, investing its posterior or postero-dorsal margin with a saddle-shaped flare. In the Saxicavidae and Laternulidae the gastric shield barely touches the posterior border of the left pouch. In the Unionidae and Lucinidae the gastric shield does not reach the left pouch. In the Cyamiidae and Ungulinidae there was no indication of the presence of a left pouch (the specimens studied were very small and a small left pouch could easily have been overlooked). It is possible that in a small species the stomach may be simplified with the accompanying loss of certain structures.

4. *The entry of ducts from the digestive diverticula.* It is not always easy to define with precision the ventral or median border of the left pouch, and in such cases the number of ducts which may be regarded as opening within its confines may be doubtful. The chief function of the left pouch is probably to aid in giving the gastric shield a firm anchorage. No functional advantage arises from the proximity of the orifices of the ducts to the margin of the gastric shield, nor from their location within the left pouch rather than just outside the left pouch. There is therefore no reason why variability in this feature should have any significance.

Various degrees of concentration of the ducts are recorded in the twenty-one families under consideration. As many as nine ducts enter the left pouch in the Limidae, and six in the Pectinidae ; typically there are from three to

five such ducts, but there are only two in the Unionidae and in the Myochamidae, only one in the Trigoniidae and Chamostreidae, and apparently none in the Astartidae, Pandoridae, and Laternulidae. No data are available for the Cyamiidae, Montacutidae and Ungulinidae due to the small size of the specimens studied.

The digestive diverticula probably opened into the stomach primitively by numerous scattered orifices, and this condition still occurs in the Pectinidae, Anomiidae, Chamidae and, to a lesser extent, in the Carditidae. An advance is seen in the Limidae where the orifices of the ducts are gathered together into three compact groups. In other families there has probably been a process of concentration of the ducts, giving increased protection to the digestive diverticula from the arrival of excessive quantities of particulate matter. This process appears to have occurred independently on the left and the right sides of the stomach. In several families numerous ducts open into a deep recess formed by embayment of the left anterior floor of the stomach, e.g. the Pandoridae, Laternulidae, Chamostreidae, Myochamidae, Chamidae, Unionidae and Gastrochaenidae, and in the last three examples this deep embayment is penetrated by the major intestinal typhlosole and intestinal groove, and could therefore be directly compared with the left caecum of the Pholadidae (Purchon, 1955), a structure which is characteristic of Stomach Type V, shortly to be described.

In many families there has been concentration of the ducts entering the right side of the stomach. The Erycinidae appear to be primitive in possessing a cluster of about ten ducts on the right side. In the Lucinidae there are only three slender ducts on the right side, but these ducts are very simple in appearance, and the small number does not seem to have been produced by fusion of ducts. In the Saxicavidae, Unionidae, Myochamidae and Gastrochaenidae there are only one large and one small duct on the right side, while there is only one single duct on the right side in the Sphaeriidae, Astartidae, Pandoridae, Laternulidae and Chamostreidae.

The greatest simplicity of form is reached in the Trigoniidae, Laternulidae, Cyamiidae, Montacutidae and Ungulinidae, where the digestive diverticula open into the stomach by only two orifices other than the left pouch. In the last three of these families this simplicity may partly derive from the small size of the species.

5. *The distribution of the sorting areas of the stomach.* Undoubtedly the disposition of the sorting areas of the stomach has a greater superficial effect on its internal appearance than has any other variable feature. It is possible that in some cases two sorting areas may come into contact and, perhaps by some integrating action, harmonise with each other so that the presence of two components is not clear ; it might then appear that one sorting area or the other has extended its range and its functions to embrace that of the other. Analysis of these sorting areas is therefore not without difficulty and danger of mistake. The following sorting areas have been recognised ; they have been given the same labels, wherever possible, as in previous papers (Purchon, 1956, 1957).

a. *The anterior sorting area* (SA). This is found on the anterior floor of the stomach and consists of parallel ridges and grooves running towards the intestinal groove. It is particularly well developed in the Pectinidae, Limidae and Anomiidae (where it is divided into two parts) ; it is moderately well developed in the Chamidae, Pandoridae, Myochamidae, Laternulidae and Chamostreidae ; traces of it can be found in the Trigoniidae and Unionidae. It is absent from a group of families in which the species are of small size. A sorting area in a similar position, but on which the cilia beat in the opposite direction, i.e. towards the oesophagus, is treated separately (SA^7).

b. *The principal sorting area of the dorsal hood* (SA^3). This lies on the anterior face or roof of the dorsal hood and on it cilia beat transversely over the crests of the folds towards the apex of the dorsal hood. The area typically extends over the roof and on to the right side of the stomach. It is accompanied on its anterior side by a rejection groove which discharges into the intestinal groove (The Myochamidae appear to be exceptional). The sorting area is well developed in the Trigoniidae, Unionidae, Pandoridae and Laternulidae ; it is moderately well developed in the Chamidae and Saxicavidae, while in the Sphaeriidae, Gastrochaenidae and Chamostreidae it is well developed only within the dorsal hood. It is not found in a number of families with specimens of small size, but it is also notably absent from the Pectinidae, Limidae, Anomiidae and Carditidae.

c. *A second sorting area on the anterior side of the dorsal hood* (SA^4). This consists of a narrow belt of transverse ridges and grooves which curves downwards and terminates close to the mouth of the left pouch. It only occurs in the Pectinidae, Limidae and in *Placuna* in the Anomiidae.

d. *The sorting area on the posterior wall of the dorsal hood* (SA^5). This curves backwards out of the dorsal hood on to the posterior wall of the stomach. It has only been recorded in *Placuna* in the Anomiidae, in the Carditidae, Chamostreidae and Laternulidae.

e. *The sorting area of the left pouch* (SA^6). In the Carditidae and Chamidae this is confined to the left pouch ; in the Saxicavidae and Gastrochaenidae it covers the floor of the left pouch and is confluent with a sorting area which lies below the orifice of the oesophagus, and from which it may have been derived. In the Erycinidae there are a few broad and irregular folds on the floor of the left pouch which may be termed a sorting area.

f. *The sorting area below the orifice of the oesophagus* (SA^7). Here ciliary currents are directed forwards towards the oesophagus and not towards the intestinal groove and not transversely to the left over the crests of the folds, as on the anterior sorting area (SA). This sorting area is well developed only in the Carditidae, Saxicavidae, Gastrochaenidae and Chamostreidae. It is relatively small in the Unionidae and in the Chamidae. In the Erycinidae it is presumably represented by a number of large and irregular folds on the anterior face of the stomach.

g. *The sorting area on the anterior roof of the stomach* (SA^8). This may occur on one or on both sides of a ridge which passes backwards into the dorsal hood and along which there is a backwardly directed ciliary current. It is

particularly well developed in the Saxicavidae, and is also well shown in the Trigoniidae, Astartidae, Chamidae, Gastrochaenidae, Laternulidae, Myochamidae and Chamostreidae. It is less well developed in the Unionidae, where its association with the dorsal hood is not well displayed. It is probably present in the Carditidae, though in that family it is not easy to decide what components are to be recognised in the large sorting area on the anterior face of the stomach. There was no sign of this sorting area in various families with specimens of small size, but it was also notably absent from the Sphaeriidae and Pandoridae.

h. *The Right Posterior Sorting Area* (SA^9). This has been found only in the Laternulidae, and may be a special development of the principal sorting area of the dorsal hood (SA^3).

These variations are set out in Table 1, in which the atypical cases are clearly indicated (⊕). Previous authors have found difficulty in separating the main body of the Filibranchia from the Eulamellibranchia. Thus Pelseneer (1906) followed Ridewood (1903) in assigning the Pinnidae, Ostreidae and Limidae to the Eulamellibranchia (=Synaptorhabda) though he later (1911) returned these three families to an intermediate group, the Pseudolamellibranchia. Thiele (1934) placed the filibranch family Trigoniidae in the Eulamellibranchia. It was therefore of particular interest to determine whether the Pectinidae, Limidae, Anomiidae and Trigoniidae harmonise with the sixteen eulamellibranch families here under consideration, or whether they constitute an intermediate group between the Eulamellibranchia and the main body of the Filibranchia as regards the internal structure of the stomach. It was concluded from the present survey that there is no single anatomical criterion of sufficient significance to justify dividing these twenty-one families into two or more groups of families. Nor is it possible to justify a phylogenetic division on the basis of an accumulation of evidence from items individually trivial but collectively significant. As regards the internal structure of the stomach the twenty-one families here under consideration comprise a homogeneous and possibly monophyletic group.

Some of the evidence presented in this paper may have a bearing on the subsequent phyletic subdivision of the group. Thus the Erycinidae and Montacutidae, and perhaps also the Cyamiidae, may have a common ancestry as indicated by separation of the style-sac and mid-gut in these families. Again, the possession of the second sorting area of the dorsal hood by the Pectinidae, Limidae and Anomiidae might also indicate that these three families are particularly closely related to each other.

The evidence adduced in the present paper, combined with that recorded previously (Purchon, 1957) appears to indicate that the Limidae, Pectinidae and Anomiidae would best be transferred out of the Anisomyaria (Thiele, 1934) to join the Trigoniidae in the order Eulamellibranchia ; this order should then be renamed since some of its constituents would not possess eulamellibranch ctenidia. It remains to be demonstrated in a subsequent paper that in a considerable number of families in the Eulamellibranchia the interior of the stomach fits a different plan and can be assigned to Stomach Type V. By the

Analysis of variation

		Anomiidae
1	The style-sac and mid-gut are conjoined The minor typhlosole is typical	
	The style-sac and mid-gut are separate The minor typhlosole is absent	⊕
2	The major typhlosole and intestinal groove end on the stomach floor, near the openings of ducts from the digestive diverticula	+
	The major typhlosole and the intestinal groove end just within the left pouch	+
	The major typhlosole and the intestinal groove penetrate deeply into an embayment adjacent to the left pouch	
	The major typhlosole and the intestinal groove terminate in a tight spiral on the floor of the stomach	
3	The gastric shield invests the border of the left pouch	+
	The gastric shield just touches the posterior border of the left pouch	
	The gastric shield does not reach the left pouch	
4	The orifices of ducts from the digestive diverticula are numerous and scattered	⊕
	The orifices of ducts from the digestive diverticula are fewer in number and may be somewhat concentrated	
	The orifices of ducts from the digestive diverticula are very few in number	+
5	The following sorting areas are present :	
	SA On the anterior floor of the stomach	+ (+
	SA^3 On the roof or anterior side of the dorsal hood and sometimes extending over the right wall of the stomach	+
	SA^4 On the anterior face of the dorsal hood, and extending down towards the left pouch	⊕
	SA^5 On the posterior wall of the dorsal hood	+
	SA^6 In the left pouch	
	SA^7 Immediately below the oesophageal orifice	
	SA^8 On the anterior roof of the stomach, leading back from the oesophageal orifice into the dorsal hood	+
	SA^9 On the right posterior wall of the stomach	

(+) means somewhat
⊕ indicates as aty

re of the stomach

Anomiidae	Trigoniidae	Unionidae	Astartidae	Carditidae	Sphaeriidae	Cyamiidae	Erycinidae	Montacutidae	Ungulinidae	Lucinidae	Chamidae	Saxicavidae	Gastrochaenidae	Pandoridae	Laternulidae	Chamostreidae	Myochamidae	Clavagellidae
	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+
⊕						⊕	⊕	⊕										
+	+		+		+	+	+			+		+		+	+	+	+	
+								+										
		⊕									⊕		⊕					
				⊕														
+	+		+	+	+		+	+			+		+	+		+	+	+
												⊕			⊕			
		⊕								⊕								
⊕											⊕							
				+			+			+		+	+	+				
	+	+	+		+	+		+	+						+	+	+	+
+	(+)	(+)									+		?	+	+	+	+	+
	+	+			+				?		+	+	+	+	+	+	+	+
⊕																		
+				+											(+)	+		
				+			+				+	+	+					
		(+)		+			+				(+)	+	+			+		
	+	(+)	+	+							+	+	+		+	+	+	
															+			

(+) means newhat reduced.
⊕ indicates d as atypical features.

possession of a stomach either of Type IV or of Type V, the Eulamellibranchia (emended as indicated above, and suitably renamed) can be subdivided into two natural groups, each of which may well be monophyletic.

SUMMARY

1. The internal structure and function of the stomach is described for representatives of seventeen families of Eulamellibranchia.

2. Detailed comparisons are made among these and comparable data previously obtained from four families in the Filibranchia and Pseudolamellibranchia, and it is concluded that there are no grounds for sub-dividing these twenty-one families into two or more groups. In all cases the stomach is of Type IV.

3. A new definition for Stomach Type IV is provided.

4. It is concluded that on the basis of the internal structure of the stomach these twenty-one families appear to comprise a natural and monophyletic assemblage.

REFERENCES

Allen, J. A. (1954). On the structure and adaptations of *Pandora inaequivalvis* and *P. pinna*. *Quart. J. micr. Sci.* **95,** 473–482.

Allen, J. A. (1958). Observations on *Cochlodesma praetenue* (Pulteney) [Eulamellibranchia]. *J. mar. biol. Ass. U.K.* **37,** 97–112.

Graham, A. (1949). The molluscan stomach. *Trans. Roy. Soc. Edinb.* **61,** 737–778.

Gutheil, F. (1912). Über den Darmkanal und die Mitteldarmdrüse von *Anodonta cellensis* Schröt. *Z. wiss. Zool.* **99,** 444–538.

Oldfield, E. (1955). Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius). *Proc. malac. Soc. Lond.* **31,** 226–249.

Pelseneer, P. (1906). *A treatise on zoology.* Part 5, Mollusca. London : A. and C. Black.

Pelseneer, P. (1911). Les lamellibranches de l'expedition du siboga. Partie Anatomique. *Siboga Exped. Monogr.* No. 53 a.

Purchon, R. D. (1955). A note on the biology of *Tridacna crocea* Lam. *Proc. malac. Soc. Lond.* **31,** 95–110.

Purchon, R. D. (1956). The stomach in the Protobranchia and Septibranchia (Lamellibranchia). *Proc. zool. Soc. Lond.* **127,** 511–525.

Purchon, R. D. (1956 a). A note on the biology of *Brechites penis* (L.). *J. Linn. Soc. Lond.* **43,** 43–54.

Purchon, R. D. (1957). The stomach in the Filibranchia and Pseudolamellibranchia. *Proc. zool. Soc. Lond.* **129,** 27–60.

Ridewood, W. G. (1903). On the structure of the gills of Lamellibranchs. *Phil. Trans.* (B) **194,** 194–284.

Thiele, J. (1934). *Handbuch der systematischen Weichtierkunde.* Teil 3. Jena : Fisher.

Winckworth, R. (1932). The British marine mollusca. *J. Conch.* **19,** 211–252.

KEY TO THE LETTERING OF THE FIGURES

B	Blind pocket on right side of stomach (*Myadora*).
C	Conical protuberance on the floor of the stomach (*Anodonta*).
CS	Crystalline style.
D	Depression in the right wall of the stomach (*Chama*).
DH	Dorsal hood.
DDD, DDD$^{1-8}$	Orifices of ducts from the digestive diverticula.
F	Folds on the anterior wall of the stomach (*Thyasira*).
G	Groove on the floor of the stomach (*Pandora*).
G^1	Ciliated groove on the right wall of the stomach (*Astarte*).
GS	Gastric shield.
H	Hollow projecting backwards from the mouth of the dorsal hood (*Beguina*).
IG	Intestinal groove
LP	Left pouch
MG	Orifice of mid-gut.
MT	Minor typhlosole.
O	Orifice of the oesophagus into the stomach.
P	A raised pad on the right wall of the stomach (*Montacuta*, *Hiatella*, *Pandora*).
R	A ridge passing from the oesophageal orifice over the roof to the dorsal hood.
R^1	A ridge passing to the dorsal hood from the sorting area on the anterior floor of the stomach (*Scintilla*).
R^2	A ridge, or ridges on the posterior wall of the dorsal hood.
RM	A rim around the opening of the oesophagus into the stomach.
RT	A ciliated rejection tract leading from the dorsal hood to the intestinal groove.
RV	The rim of the vestibule (*Chama*).
SA	A sorting area on the anterior floor of the stomach, which discharges waste into the intestinal groove.
SA^3	A sorting area in the dorsal hood, which may extend over the right side of the stomach.
SA^5	A sorting area on the posterior wall of the dorsal hood.
SA^6	A sorting area in the left pouch.
SA^7	A sorting area lying just below the orifice of the oesophagus.
SA^8	A sorting area on the roof of the stomach.
SA^9	A sorting area on the right posterior wall of the stomach (*Laternula*).
SF	A spiral fold formed by the major typhlosole and the accompanying intestinal groove (*Beguina*).
SS	The orifice of the style-sac.
T	Prominent tooth on gastric shield (*Myadora*).
TY	The major typhlosole.
V	The vestibule, or anterior chamber of the stomach (*Chama*, *Cleidothearus*).

EASTBOURNE MARINE SHORE FAUNA

Being notes on the distribution of species occurring in the neighbourhood of the Beachy Head and Holywell areas of Eastbourne

BY

A. R. PAUL, M.Sc., F.Z.S.

Biology Dept., Quintin School, London, N.W.8

[Accepted 11th February 1958]

(With 1 figure in the text)

CONTENTS

	Page
Introduction	528
Description of methods	528
Geology of the Eastbourne coastline	528
Descriptions of the collecting grounds	532
Phylum Porifera	533
Bibliography	534
Phylum Coelenterata	534
Bibliography	536
Phylum Platyhelminthes	536
Bibliography	537
Phylum Nemertinea	537
Bibliography	538
Phylum Annelida	538
Bibliography	540
Phylum Arthropoda	540
Sub-Phylum Crustacea	540
Bibliography	545
Sub-Phylum Insecta	545
Bibliography	546
Phylum Mollusca	546
Bibliography	550
Phylum Polyzoa s. str.	550
Phylum Kamptozoa	551
Bibliography	551
Phylum Echinodermata	551
Bibliography	552
Phylum Chordata	552
Sub-Phylum Tunicata	552
Bibliography	553
Sub-Phylum Vertebrata	553
Bibliography	555
Appendix I List of Algae	555

* The classification followed in this paper is taken from "Plymouth Marine Fauna" 3rd edition published by the Marine Biological Association 1957, by permission of the Director: F. S. Russell, C.B.E., D.S.C., D.F.C., LL.D., F.R.S.

INTRODUCTION

During the summer of 1951, while a student at Reading University, I commenced a survey of the Eastbourne shore fauna. Collecting was continued during the summer months of subsequent years and this paper contains the results of such collecting.

I was unable to compare these results with any compiled by earlier workers as no faunal list was available for this part of the coast. However, there were a few lists of individual phyla in existence the majority of which were of considerable age and dealt with areas near, though outside Eastbourne: for example the Diamond Grounds of Hastings and the Black Rock area of Brighton. These lists, however, do have a certain comparative value because if a certain species had previously been recorded near Eastbourne there was a strong possibility of it occurring at Eastbourne. The only local list that I have so far come across is one of hydroids compiled about 1880, this list contains some eighty species but lacked any information with regard to the exact locality where species were found, and, which is most important, whether or not they were found attached.

The main aim of this survey was not to obtain a complete list of the shore animals of the area but to compile a basic list. The locality selected for this was that portion of the rocky shore situated between Beachy Head and Holywell. Such a list would then serve as one of reference for future work in adjacent areas.

Prior to listing the fauna, a brief geological description of the Eastbourne coastal area is given, together with a description of the main collecting areas. The classification and arrangement of the species follows the order used in the Plymouth Marine Fauna List, third edition, 1957. It was found more convenient to list references at the end of each phylum.

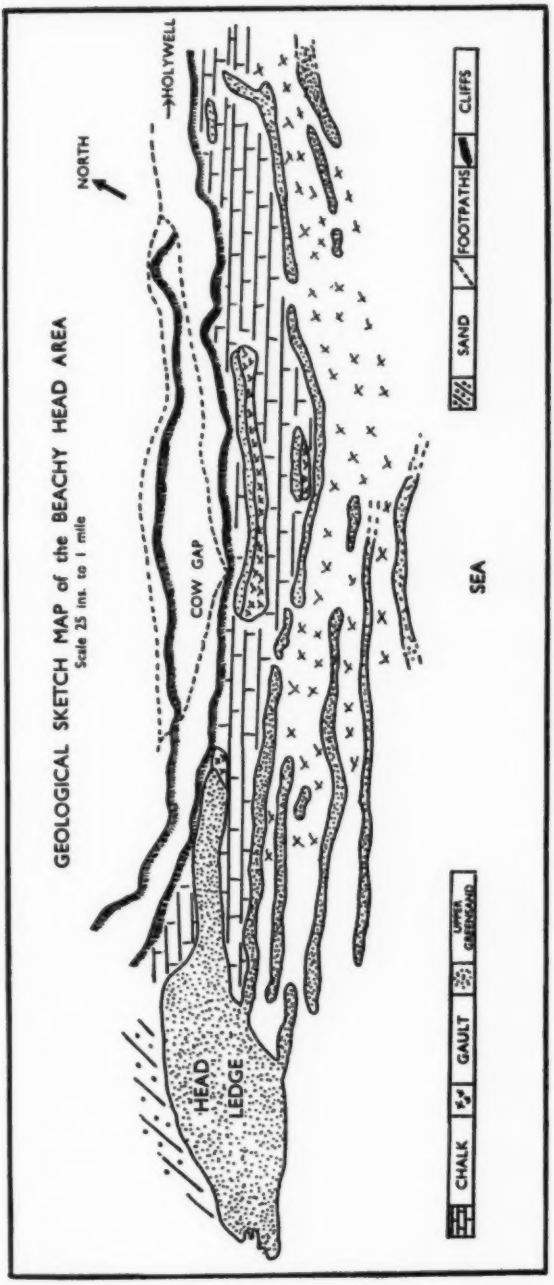
METHODS

Collecting was carried out over the area at low tide, the majority of the specimens being collected by hand or by means of a small hand net. No particular section of the shore was concentrated upon as the idea was to give as general a picture of the fauna as possible. No plankton netting was carried out, which helps to explain the absence from the list of so many of the animals normally collected in this manner. It is hoped to rectify this in the near future.

The material thus collected was identified with the aid of the literature listed after each phylum. A diagramatic map of the area based on the Ordinance Survey sheet appears on page 529.

GEOLOGY OF THE EASTBOURNE COASTLINE

The cliffs of Beachy Head rise up to a height of some five hundred feet from the middle shore platform. They are composed mainly of upper, middle and lower chalk; the dip is to the west. At the eastern end the hard subglobosus chalk is conspicuous at the base, in front of this harder bands of " varians " chalk form a series of north to south lines in the shore platform below the shingle. The cliffs are almost vertical, and in some places overhang:


GEOLOGICAL SKETCH MAP of the BEACHY HEAD AREA
Scale 25 ins. to 1 mile
NORTH
HOLYWELL
COW GAP
HEAD
LEDGE
SEA
CHALK
GAULT
UPPER GREENSAND
SAND
FOOTPATHS
CLIFFS

the flint lines are well shown. Erosion has taken place along the joint planes forming what are known as " chimneys ".

The straight line of the cliffs extending from the headland to Eastbourne is of varying character. It appears to have formed part of a chalk escarpment, the trend of which, where two coombs replace the vertical cliffs, is approximately north to south as opposed to the general east to west trend of the Weald. The dip is inwards so this part is synclinal. The sea in cutting into these escarpment-like slopes has formed low cliffs, which, vary in height from twenty to seventy feet. It is in these low cliffs and the shore platform below that the complicated structures in the Lower Chalk, Upper Greensand and Gault are exposed. Behind Cow Gap, an inland cliff some seventy feet high extends for some distance parallel to the low sea cliff, the former cuts into the slope. Boulders and scree at its foot are due to erosion and subsequent slipping.

The westerly dip of the beds at the headland exposes at the angle of the cliffs a fine outcrop of Upper Greensand as a reef, " The Head Ledge." Disturbance of the beds is noticeable north of this ledge though in many places the scour of the sea has obscured the boundaries of the softer rocks. Elsewhere, especially where the strata was thin, all traces of this disturbance has been removed by such action. In a similar manner indications of the thrust has in many places been obliterated.

The Head Ledge curves towards the cliffs in a manner suggesting a pitching anticline. The lower part, however, is cut off by a thrust plane and only about fifteen feet of the Upper Greensand remains, this also soon disappears into the cliff. Here, due to faulting, the Lower Chalk is in contact with the Greensand, except at the northern end where the upper part of the Greensand rests upon Gault.

From the main mass of the reef there extend two narrow reefs, both of which are slightly concave, towards the cliffs. The first of these is, except for three short gaps, continuous along the coast as a narrow outcrop, while the second striking out from The Head Ledge soon ends. Further outcrops of Greensand do occur to the east in such a manner as to suggest that at one time they were continuous with this second reef. There is a third reef but this is difficult to examine, as, even at very low tide, it is not completely exposed. Except for a few short gaps, it appears to be continuous along this region of the coast and running almost parallel to the first two reefs. There are, near the base of the cliffs, rows of blocks of Greensand stranded upon Gault which simulate reefs, most of these are narrow, so it seems that the complete thickness of the Greensand in this area is not revealed. There are hard cherty bands present which form conspicuous features at the cliff end of The Head Ledge, these may well have played a part in the formation of the reefs.

Near where the footpath comes down to the beach at Cow Gap, Upper Greensand reappears, this exposure continues eastwards along the base of the cliffs for about a thousand yards, where it then dips into the cliffs. A short distance from this point there are two further exposures of Greensand at the base of the cliffs, these also soon dip into the cliffs. Lower Chalk occurs below this outcropping Greensand.

Gault generally occurs where expected below the Greensand, though the

bedding plane is not always clear. Where this Gault is exposed on the shore it is heavily eroded, this, no doubt, is aided by the heavy boring of such animals as *Pholas dactylus* L.

The Beachy Head area is therefore a disturbed one, probably so as a result of Alpine folding and local compression, this may account for the breaking up of the inclined sheets of Greensand thus enabling the softer Gault and Chalk to flow round them at the time of formation.

From Beachy Head to Holywell " plenus marls " occur on top of the Lower Chalk, these slope eastwards and eventually reach the beach where they throw out several fresh water springs. These marls are easily eroded by wave action thus enabling the sea to undermine the cliffs, and, as a result of this activity, varying amounts of shattered rock lie at the base of the cliffs in this area. The hard rough Chalk of the " cuveri " zone is well seen in places above the " plenus marl ".

As a result of building, especially of the promenades, very little of the geology of the actual Eastbourne front can now be seen. There is however, Upper Greensand occurring below the Wish Tower, where in places the base of the Lower Chalk can also be seen. In this area there is a considerable accumulation of chalk rubble probably of glacial origin.

Beyond Eastbourne there occurs a very remarkable accumulation of shingle known as the " Crumbles ". This consists of an almost flat expanse in which a number of slightly raised beaches or ridges occur. These lines are almost parallel and curve a little towards the east, this being more noticeable towards Pevensey Bay. These ridges can be traced for almost a mile though some of them fade out *en route*. In all probability they are storm beaches that have been thrown up successively until at its widest point the beach is almost one mile across.

The material comprising the beach is mainly flint, but there are also numerous pebbles of Greensand, Chert and Hard Chalk. In size these pebbles appear to diminish as one proceeds northeastwards along the shore. On searching, pebbles of other material can be found. It seems evident that the material comprising the " Crumbles " has been derived from the west as a result of along-shore drift, there are several factors in support of this:—

1 Pebbles can be found of quartzes and quartztourmaline very similar to the rocks and cliffs of that material occurring in Devon and other localities in the west.

2 The tides which break upon the Eastbourne beach have a slight inclination to the east. This can be seen particularly well after a period of heavy seas during which shingle is scoured by the tides from the western sides of the groynes and deposited on the eastern side; thus indicating an alongshore movement of shingle. (For a number of years new groynes have been constructed in order to prevent this movement of shingle with, as yet, little visible signs of success.)

Behind the " Crumbles " there is an expanse of alluvium, The Levels. Wadhurst Clay is also present and is exposed to the east of the " Crumbles " as isolated areas of soft rock. It is possible that such rocks occur to the seaward of this area as well.

THE COLLECTING GROUNDS

The majority of the specimens were collected from the shore between the western end of the promenade at Holywell and the stretch of sand west of The Head Ledge. The area was not rich in species, and many were not found in large numbers. General collecting only was carried out, as mentioned on page 528.

The section of the shore concerned is essentially of a rocky nature, sand is somewhat limited, occurring mostly in small isolated patches, the largest single expanse being just west of The Head Ledge. A shingle beach extends for some twenty yards down the shore from the base of the cliffs at the eastern end of the area, the depth of this fluctuates as one proceeds towards The Head Ledge where it is reduced to a few yards. This is mainly due to wave erosion and the covering of the shingle by cliff falls. As one proceeds in a westerly direction the amount of this chalk scree also varies, as does the extent of bare rock which is mostly Chalk, Greensand and Gault.

The shore slopes gently seawards, the rock strata being almost horizontal. Zonation is, as a result, not clearly defined, in spite of this, the characteristic zonation of the littoral zone can be discerned at the eastern extremity of the collecting area with a reasonable degree of accuracy. There is a narrow though definite splash zone characterised by the green alga *Enteromorpha intestinalis*, the numerous fresh water springs issuing from the base of the cliffs in this area no doubt have an effect upon this zone. Towards the lower extremities of the zone are found *E. compressa* and *Cladophora rupestris*. Several of the animals normally associated with this zone were recorded: *Ligia oceanica*, *Talitrus saltator*, *Orchestia gammarella*, *Gammarus locusta* and *Littorina neritoides*. Due once again in all probability to the abundance of freshwater in this area, the second zone characterised by the green alga *Ulva lacuta* was not clearly differentiated. Where *Ulva* was in abundance *Littorina neritoides*, *L. saxatilis*, *Patella vulgata* and *Balanus balanoides* were common. The *Fucus* zone, however, was more clearly differentiated, though broken at frequent intervals by narrow belts of sand or zones of deeper water, no doubt due to the erosion of the softer rocks, in the latter the dominant weed was often *Laminaria*. As a result of this the dividing line between the *Fucus* and *Laminaria* was far from clear, though the true zone of the latter in all probability begins in the deeper waters near the Outer Reef. In the main area of the *Fucus* zone the common species of *Fucus* were found together with *Ascophyllum nodosum*. Many of the animals associated with this zone were also found: *Littorina littoralis*, *L. littorea*, *Gibbula umbilicalis*, *Chitons*, *Leucosolenia* spp, *Grantia compressa*, *Halichondria panicea* and *Actinia equina*. In the deeper waters associated with *Laminaria* were found *Halisarca dujardini*, *Oscarella lobularis*, *Ophilataspongia seriata*, *Crisia cornuta* etc.

At low tide the *Fucus* and *Laminaria* were found attached to the Chalk and Gault and occasionally to isolated boulders of Greensand. Areas of the Gault and in some instances the chalk were seen to be heavily bored by *Pholas*.

In amongst these main areas of the littoral zone there occur numerous isolated areas of sand, fine shingle, muddy sand and in some places soft mud

formed as a result of the breakdown of Gault, in such areas animals characteristic of such habitats were usually found though generally in small numbers.

The whole area is subjected to considerable wave action, the reefs, particularly the Outer one do, however, provide some protection from the prevailing winds and high seas, although such protection is essentially restricted to low tide. The reefs themselves tend to be devoid of weeds on the seaward side, although young plants of *Fucus* and *Laminaria* are to be found growing on the sheltered side, some are to be found on the seaward side, these generally do not reach maturity to such an extent as those on the sheltered side. Crevices on both sides of the reefs, more especially those on the sheltered side were found to provide shelter for numerous crevice animals.

Phylum **PORIFERA**

Class CALCAREA

Family **Homocoelidae**

LEUCOSOLENIA COMPLICATA (Montagu) 1818, p. 97.

Several specimens in rock-pools between tide-marks; Head Ledge to Holywell.

Family **Sycettidae**

SYCON CORONATUM (Ellis and Solander) [*Bowerbank*, 1866, p. 19, as *Grantia ciliata*]

A few specimens at extreme low-water near Head Ledge. (Crawshay, 1912, p. 303 regards this species and *S. ciliatum* as synonymous.)

Family **Grantiidae**

GRANTIA COMPRESSA (Fabricius) [*Bowerbank*, 1874, p. 1 and *Arndt*, 1934, p. 15]

Common on rocks between tide-marks and at low-water; Head Ledge to Holywell.

Class DEMOSPONGIARA

Order *TETRACTINOMORPHA*

Sub-Order *HOMOSCLEROPHORA*

Family **Oscarellidae**

OSCARELLA LOBULARIS (O. Schmidt) [*Arndt*, 1934, p. 23]

Several specimens between tide-marks; Head Ledge.

Family **Clavulidae**

CLIONA CELATA Grant [*Arndt*, 1934, p. 44]

Boring in dead *Pectin* shells very common, also in Chalk and Gault of Inter-tidal zone; Holywell.

Order *CERATINOMORPHA*

Sub-Order *HALISARCIDA*

Family **Halisarcidae**

HALISARCA DUJARDINI Johnston, 1842, p. 192 [*Arndt*, 1934, p. 109]
Several specimens incrusting upon rocks, also on *Carcinus*; Head Ledge to Holywell.

Sub-Order *HALICHONDRINA*

Family **Haploscleridae**

HALICLONA OCULATA (Pallas) [*Arndt*, 1934, p. 100]
Several unattached specimens stranded at low-tide Holywell.

Family **Desmacidonidae**

Sub-Family Clathriinae

MICROCIONA ATRASANGUINEA Bowerbank [*Arndt*, 1934, p. 78]
Encrusting on rocks of mid-tidal zone; Head Ledge to Holywell.
OPHLITASPONGIA SERIATA (Grant) [*Arndt*, 1934, p. 82]
Several encrusting patches on reefs; Holywell. Between tide-marks Head Ledge.

Sub-Family Halichondriinae

HALICHONDRIA PANICEA (Pallas) [*Arndt*, 1934, p. 103]
Common on rocks in all zones; Head Ledge to Holywell.

BIBLIOGRAPHY

ARNDT, W. (1934). Porifera. *Tierwelt N.-u. Ostsee*, Teil 3, a 1; 1-102 (Lief. 27).
BOWERBANK, J. S. (1864-1882). *A. monograph of the British Spongidae* **1,** (1864), 290 pp.; **2,** (1866) 388 pp.; **3,** (1874), 367 pp.; **4,** (1882), 83 pp. London: Ray Society.
BURTON, M. (1930). Additions to the sponge fauna at Plymouth. *J. mar. biol. Ass.* U.K. **16,** 489.
JOHNSTON, G. (1842). *A history of British sponges and lithophytes.* 264 pp. Edinburgh.
MONTAGU, G. (1818). An essay on sponges, etc. *Mem. Werner. nat. hist. Soc.* **11,** 67.

Phylum **COELENTERATA**

Class HYDROZOA

Order *HYDROIDA*

Sub-Order *ANTHOMEDUSAE*

Family **Tubulariidae**

TUBULARIA INDIVISA L. [*Allman*, 1871, p. 400]
On Outer Reef Holywell: in low-tide rock-pools Holywell and Head Ledge.
TUBULARIA LARYNX Ellis and Solander [*Allman*, 1871, p. 406]
On *Laminaria* and rocks of the Outer Reef; Holywell.

Family **Corynidae**

CORYNE PUSILLA Gaertner [*Hincks*, 1868, p. 41; as *C. vaginata; Allman*, 1871, p. 268; as *C. vaginata*]
Common in pools between tide-marks; Holywell to Head Ledge.

Family **Clavidae**

CLAVA MULTICORNIS (Forskål) [*Allman*, 1871, p. 246]
Common on stones in rock-pools; Holywell.
CLAVA SQUAMATA (O. F. Müller) [*Allman*, 1871, p. 243]
Common, especially on *Fucus* between tide-marks; Head Ledge to Holywell.

Family **Bougainvilliidae**

BOUGAINVILLIA RAMOSA (Van Beneden) [*Allman*, 1871, p. 311] (Medusa, *B. ramosa*)
Few colonies on reefs; Holywell.
GARVEIA NUTANS Wright [*Allman*, 1871, p. 295]
Several colonies on rocks particularly towards low-tide mark; Head Ledge.

Sub-Order *LEPTOMEDUSAE*

Family **Campanulariidae**

CLYTIA JOHNSTONI (Alder) [*Hincks*, 1868, p. 143] (Medusa, *Phialidium hemisphaericum*)
Fairly common on seaweeds of intertidal region; Head Ledge to Holywell.
OBELIA GENICULATA (L.) [*Hincks*, 1868, p. 149]
Very common especially on *Laminaria* and *Fucus* spp; Head Ledge to Holywell.

Family **Sertulariidae**

DYNAMENA PUMILA (L.) [*Hincks*, 1868, p. 260, as *Sertularia*]
Common on rocks and weeds between tide-marks; Head Ledge to Holywell.
SERTULARIA OPERCULATA (L.) [*Hincks*, 1868, p. 263]
Several colonies on *Fucus* sp; Holywell.

Class HYDROZOA

Order *SEMAEOSTOMAE*

Family **Aureliidae**

AURELIA AURITA (L.) [*Mayer*, 1910, p. 623]
Several specimens beyond the reefs.

Class ANTHOZOA

Sub-Class OCTOCORALLIA (ALCYONARIA)

Order *ALCYONACEA*

Family **Alcyonidae**

ALCYONIUM DIGITATUM (L.) [*Hickson*, 1895, p. 349]
Several specimens and part specimens washed up near Head Ledge.

Order *GORONACEA*

Family **Plexauridae**

EUNICELLA VERRUCOSA (Pallas) [Koch, 1887, p. 58, as *Gorgonia cavolini*; *Thomson*, 1912, p. 482]
On rocks near low-water; Head Ledge.

Sub-Class HEXACORALLIA

Order *ACTINIARIA*

Family **Actiniidae**

ACTINIA EQUINA L. [*Stephenson*, 1935, p. 113]
Common on rocks between tide-marks: Holywell to Head Ledge.

ANEMONIA SULCATA (Pennant) [*Stephenson*, 1935, p. 124]
Common on rocks between tide-marks; Holywell to Head Ledge.

TEALIA FELINA (L.) var. coriacea (Cuvier) [*Stephenson*, 1935, p. 139]
Fairly common on rocks between tide-marks; Head Ledge.

Family **Hormathiidae**

CALLIACTIS PARASITICA (Couch) [*Stephenson*, 1935, p. 233]
Moderately common, associated with *Eupagurus bernhardus*.

Family **Sagartiidae**

SAGARTIA ELEGANS (Dalyell) [*Stephenson*, 1935, p. 306]
In the crevices of Outer Reef and on the rocks of Head Ledge.

Order *CORALLIMORPHARIA*

Family **Corallimorphidae**

CORYNACTIS VIRIDIS Allman [*Gosse*, 1860, p. 289]
Fairly common on overhanging ledges and in rock-pools. Both the emerald green and orange varieties occur. Holywell.

BIBLIOGRAPHY

ALLMAN, G. J. (1871–2). *A monograph of the gymnoblastic or tubularian hydroids.* XXIV+ 450 pp. and plates. London: Ray Society.

GOSSE, P. H. (1860). *Actinologia Britannica. A history of the British sea-anemones and corals.* 358 pp. London.

HICKSON, S. J. (1895). The anatomy of *Alcyonium digitatum*. *Quart. J. micr. Sci.* **37**, 343.

HINCKS, T. (1868). *History of British hydroid zoophytes.* **1**, 338 pp.; **2**, Plates.

KOCH, G. VON (1887). Die Gorgoniden des Golfes von Neapel. *Fauna u. Flora Neapel, Monogr.* **15**, 1.

MAYER, A. G. (1910). *Medusae of the world.* **1**, Hydromedusae, pp. 1–230; **2**, Hydromedusae, pp. 231–498; **3**, Scyphomedusae, pp. 499–735. Washington.

STEPHENSON, T. A. (1928). *The British sea anemones.* **1**, 148 pp. London: Ray Society.

STEPHENSON, T. A. (1935). *The British sea anemones.* **2**, 462 pp. London: Ray Society.

THOMSON, J. STUART. (1912). Observations on living gorgonias (*Gorgonia verrucosa*) occurring in the English Channel. *Ann. Mag. nat. Hist.* (8) **10**, 479.

Phylum **PLATYHELMINTHES**

Class TURBELLARIA

Order *POLYCLADIDA*

Family **Leptoplanidae**

LEPTOPLANA TREMELLARIS (O. F. Müller) [*Gamble*, 1893, p. 498; *Lang*, 1884, p. 476]
Common in littoral zone under stones etc. Head Ledge to Holywell.

BIBLIOGRAPHY

GAMBLE, F. W. (1893). Contributions to a knowledge of British marine Tubellaria. *Quart. J. micr. Sci.* **34**, 433.

LANG, A. (1884). Die Polycladen (Seeplanarien) des Golfes von Neapel. *Fauna u. Flora Neapel, Monogr.* **11**, 1.

Phylum **NEMERTINEA**

Class ANOPLA

Order *PALAEONEMERTINEA*

Family **Tubulanidae**

TUBULANUS ANNULATUS (Montagu) [*McIntosh*, 1873, p. 203, Pl. 8, fig. 1, as Carinella; *Bürger*, 1904, p. 14]

Several specimens along Outer Reef.

Family **Cephalotrichidae**

CEPHALOTHRIX RUFIFRONS (Johnston) [*Bürger*, 1895, p. 539, Pl. 2, fig. 24, and Pl. 7, fig. 2, as *C. bioculata* Oersted; 1904, p. 18]

Common between tide-marks in sandy areas; Head Ledge to Holywell.

Order *HETEROMERTINEA*

Family **Lineidae**

LINEUS LONGISSMUS (Gunnerus) [*McIntosh*, 1873, p. 181, Pl. IX, as *L. marinus* Montagu; *Bürger*, 1904, p. 93]

Several specimens in weed near Outer Reef.

LINEUS RUBER (Müller) [*McIntosh*, 1873, p. 188, Pl. V, fig. 2 as *L. sanguineus*; *Bürger*, 1904, p. 101]

Common between tide-marks; Head Ledge to Holywell.

Class ENOPLA

Order *HOPLONEMERTINEA*

Family **Emplectonematidae**

EMPLECTONEMA NEESI (Oersted) [*McIntosh*, 1873, p. 178, Pl. III, fig. 6, as Nemertes; *Bürger*, 1904, p. 22]

Occasional specimen in crevices on the Outer Reef.

NEMERTOPSIS FLAVIDA (McIntosh) Beaumont [*McIntosh*, 1873, p. 170, Pl. IV, fig. 1, as *Tetrastemma flavida; Beaumont*, 1900b, p. 817, as *N. tenuis;* including *N. tenuis* of Bürger, 1904, p. 26]

Common under stones between tide-marks; Holywell.

Family **Amphiporidae**

AMPHIPORUS LACTIFLOREUS (Johnston) [*McIntosh*, 1873, p. 156, Pl. I, figs. 1 and 2; *Bürger*, 1904, p. 38]

Several specimens under stones between tide-marks; Head Ledge to Holywell.

BIBLIOGRAPHY

BÜRGER, O. (1895). Die Nemertinen des Golfes von Neapel. *Fauna u. Flora Neapel, Monogr.* **22**, 1.

BÜRGER, O. (1904). Nemertini. *Das Tierreich* Lief. 20, 151 pp. Berlin.

MCINTOSH, W. C. (1873). The nemerteans. *Monograph of the British marine annelids*, 1, Part 1, pp. 1–213, London: Ray Society.

RICHES, T. H. (1893). A list of the nemertines of Plymouth Sound. *J. mar. biol. Ass. U.K.* **3**, 1.

Phylum **ANNELIDA**

Class POLYCHAETA

Family **Aphroditidae**

GATTYANA CIRROSA (Pallas) [*McIntosh*, 1900-23, **1**, 2, p. 285]
Occasionally found commensal in the tubes of *Amphitrite johnstoni*.

LEPIDONOTUS CLAVA (Montagu) [*McIntosh*, 1900-23, **1**, 2, p. 280]
Fairly common under stones, especially in the extreme low-water.

HARMOTHOË IMBRICATA (L.) [*McIntosh*, 1900-23, **1**, 2, p. 314]
Between tide-marks, more especially in the shallower water under stones. Occasionally found in association with *Laminaria*; Head Ledge to Holywell.

HARMOTHOË IMPAR (Johnston) [*McIntosh*, 1900-23, **1**, 2, p. 353 as Evarne]
Amongst mussels near extreme low-water; Holywell.

LAGISCA EXTENUATA (Grube) including *L. elisabethae*. McIntosh [*Fauvel*, 1923, p. 76]
Fairly common between tide-marks under stones; Head Ledge to Holywell.

HARMOTHOË LUNULATA (Delle Chiaje) [*McIntosh*, 1900-23, **1**, 2, p. 342]
Occasionally under stones near low-water, several specimens amongst *Laminaria* holdfasts; Head Ledge to Holywell.

HALOSYDNA GELATINOSA (M. Sars) [*McIntosh*, 1900-23, **1**, 2, p. 384]
Occasionally found under stones in the mid-tidal zone, Holywell.

STHENELAIS BOA (Johnston) [*McIntosh*, 1900-23, **1**, 2, p. 408]
Single specimen in sandy crevice on the Outer Reef.

Family **Amphinomidae**

SPINTHER MINIACEUS Grube [*McIntosh*, 1900-23, **1**, 2, p. 232]
Several red specimens on sponge *Hymeniacidon sanguinea*. Green varieties on sponge *Halichondria panicea*, all on the Outer Reef.

Family **Phyllodocidae**

EULALIA VIRIDIS (O. F. Müller) [*McIntosh*, 1900-23, **2**, 1, p. 55]
Moderately common amongst weeds and stones in the inter-tidal zone; Holywell.

Family **Syllidae**

SYLLIS (HAPLOSYLLIS) SPONGICOLA Grube [*McIntosh*, 1900-23, **2**, 1, p. 197]
Occasional specimens amongst weeds at extreme low-water; Head Ledge.

Family **Nereidae**

NEREIS PELAGICA (L.) [*McIntosh*, 1900-23, **2**, 2, p. 267]
Common amongst weeds and rocks of inter-tidal zone; Head Ledge to Holywell.

PERINEREIS CULTRIFERA (Grube) [*McIntosh*, 1900-23, **2**, 2, p. 280, as *Nereis*]
Several specimens in muddy sand of mid-tidal areas; Holywell.

Family **Nephthydidae**

NEPHTHYS HOMBERGI Lamarck [*McIntosh*, 1900-23, **2**, 1, p. 17]
One specimen in muddy sand near low-water mark; Holywell.

Family **Eunicidae**

EUNICE HARASSI Audouin and Edwards [*Fauvel*, 1923, p. 399; *McIntosh*, 1900-23, **2**, 2, p. 425, as *E. fasciata*]
Near low water mark; Head Ledge.

MARPHYSA SANGUINEA (Montagu) [*McIntosh*, 1900-23, **2**, 2, p. 442]
Fairly common in crevices; Holywell to Head Ledge.

Family **Spionidae**

NERINE FOLIOSA (Audouin and Edwards) [*McIntosh*, 1900-23, **3**, 1, p. 142]
In sand between tide-marks; Holywell.

NERINE CIRRATULUS (Della Chiaje) [*McIntosh*, 1900-23, **3**, 1, p. 148]
Common in clean sand between tide-marks; Head Ledge to Holywell.

POLYDORA CILIATA (Johnston) [*McIntosh*, 1900-23, **3**, 1, p. 198]
Between tide-marks, boring into chalk and shells of *Purpurea;* Head Ledge to Holywell.

Family **Arenicolidae**

ARENICOLA MARINA (L.) [*McIntosh*, 1900-23, **3**, 1, p. 59]
Common in sand and mud between tide-marks; Head Ledge to Holywell.

ARENICOLA ECAUDATA Johnston [*McIntosh*, 1900-23, **3**, 1, p. 72]
In gravel, normally restricted to areas between the reefs; Head Ledge to Holywell.

Family **Sabellariidae**

SABELLARIA ALVEOLATA (L.) [*McIntosh*, 1900-23, **4**, 1, p. 22]
Several colonies attached to rocks in inter-tidal rock pools; Holywell.

Family **Amphictenidae**

PECTINARIA KORENI (Malmgren) [*McIntosh*, 1900-23, **4**, 1, p. 49, as *Lagis*]
A few specimens in sandy gravel near low-water mark; Holywell; empty tubes near Head Ledge.

Family **Terebellidae**

AMPHITRITE JOHNSTONI Malmgren [*McIntosh*, 1900-23, **4**, 1, p. 117, as *A. figulus*]

In sand near low-water mark; Holywell and west of Head Ledge.

AMPHITRITE EDWARDSI (Quatrefages) [*McIntosh*, 1900-23, **4**, 1, p. 114, as *A. gigantea*]

A few specimens in muddy sand at extreme low-water mark; Holywell.

LANICE CONCHILEGA (Pallas) [*McIntosh*, 1900-23, 4, 1, p. 137]

Tubes and animals common in sandy areas between tide-marks; Head Ledge to Holywell.

Family **Sabellidae**

DASYCHONE BOMBYX (Dalyell) [*Saint-Joseph*, 1894, p. 309]

Fairly common in *Laminaria* holdfasts of the Reef areas; Holywell.

Family **Serpulidae**

SERPULA VERMICULARIS L. [*McIntosh*, 1900-23, **4**, 2, p. 353]

Few specimens from extreme low-water mark; Holywell.

POMATOCEROS TRIQUETER (L.) [*McIntosh*, 1900-23, 4, 2, p. 362]

Common on stones and some shells from mid-tidal to extreme low-water; Head Ledge to Holywell.

SPIRORBIS BOREALIS Daudin [*McIntosh*, 1900-23, **4**, 2, p. 409]

Common on weeds and stones between tide-marks; Head Ledge to Holywell.

SPIRORBIS SPIRILLUM (L.) [*McIntosh*, 1900-23, **4**, 2, p. 391]

Occasional specimens on hydroids; Holywell. Some dead specimens on stones in Head Ledge region probably washed up by the tide from deeper waters.

BIBLIOGRAPHY

FAUVEL, P. (1923, 1927). Polychètes errantes; Polychètes sédentaires. *Faune Fr.* No. 5 (1923), 488 pp.; No. 16 (1927), 494 pp.

MCINTOSH, W. C. (1900–23). *Monograph of the British marine annelids.* **1,** Part 2, 1900, pp. 217–444; **2,** 1908–10, pp. 1–524; **3,** 1915, pp. 1–368; **4,** 1922–23, pp. 1–538. London: Ray Society.

SAINT-JOSEPH (BARON DE) (1894). Les Annélides Polychètes des côtes de Dinard., Part 3. *Ann. Sci. nat.* (Zool.), (7) **17,** 1.

Phylum **ARTHROPODA**

Sub-Phylum **CRUSTACEA**

Class COPEPODA

Order *EUCOPEPODA*

Sub-Order *CALANOIDA*

Family **Calanidae**

CALANUS FINMARCHICUS (Gunnerus) [*Sars*, 1901, **4**, p. 9]

Common in rock-pools, frequently found in the canal system of sponges; Head Ledge to Holywell.

Sub-Order *CYCLOPOIDA*

Family **Ascomyzontidae**

ASCOMYZON LATUM (Brady) [*Sars*, 1915, **6**, p. 90]
Several specimens found on the sponge *Halichondria panicea* between tide-marks; Holywell.

Class CIRRIPEDIA

Order *THORACICA*

Family **Chthamalidae**

CHTHAMALUS STELLATUS (Poli) [*Darwin*, 1854, **2**, p. 455]
Occasional specimens on rocks between tide-marks; Head Ledge to Holywell.

Family **Balanidae**

BALANUS PERFORATUS Bruguière [*Darwin*, 1854, **2**, p. 231]
Abundant on rocks between tide-marks; Head Ledge to Holywell.
BALANUS BALANOIDES (L.) [*Darwin*, 1854, **2**, p. 267]
Rocks between tide-marks; Head Ledge to Holywell.

Order *RHIZOCEPHALA*

Family **Sacculinidae**

SACCULINA CARCINI Thompson [*Van Beneden*, 1861, p. 154; *Krüger*, 1927, p. 6]
Fairly common, parasitic on *Carcinus*; Head Ledge to Holywell.

Class MALACOSTRACA

Sub-Class LEPTOSTRACA

NEBALIA BIPES (Fabricius) [*G. O. Sars*, 1896, p. 9]
Fairly common under stones towards low-water mark; Head Ledge to Holywell.

Order *ISOPODA*

Sub-Order *FLABELLIFERA*

Family **Sphaeromatidae**

SPHAEROMA SERRATUM (Fabricius) [*Omer-Cooper* and *Rawson*, 1934, p. 32]
Common under stones between tide-marks, also in weeds and crevices; Head Ledge to Holywell.

Sub-Order *VALVIFERA*

Family **Idoteidae**

IDOTEA PELAGICA Leach [*Sars*, 1897, p. 81, pl. 33; *Naylor*, 1955, p. 487]
Several specimens netted amongst *Laminaria*; Outer Reef.
IDOTEA BALTICA (Pallas) [*Sars*, 1897, p. 80, pl. 32; *Naylor*, 1955, p. 491]
In rock-pools and shallow water between tide-marks amongst weed; Head Ledge to Holywell.

IDOTEA EMARGINATA (Fabricius) [*Sars*, 1897, p. 85, pl. 35(2); *Naylor*, 1955, p. 492]

Under stones between tide-marks often in association with *I. baltica*; Head Ledge to Holywell.

Sub-Order *ONISCOIDEA*

Family **Ligiidae**

LIGIA OCEANICA (Linnaeus) [*Sars*, 1898, p. 156, pl. 70]

Common amongst boulders scree and shingle and in crevices above high-water mark; Head Ledge to Holywell.

Order *AMPHIPODA*

Sub-Order *GAMMARIDEA*

Family **Gammaridae**

MARINOGAMMARUS MARINUS (Leach) [*Sexton* and *Spooner*, 1940, pp. 638-44]

Fairly common on the shore under stones between tide-marks; Head Ledge to Holywell.

GAMMARUS LOCUSTA (L.) [*Chevreux* and *Fage*, 1925, p. 257; *Sexton*, 1942, pl. 3]

Occasional specimens found among weeds between tide-marks; Holywell.

Family **Talitridae**

TALITRUS SALTATOR (Montagu) [*Sars*, 1890, p. 23, pl. 9; *Chevreux* and *Fage*, 1925, p. 271]

Common in sandy areas under stones, especially near high-water mark west of Head Ledge.

ORCHESTIA GAMMARELLA (Pallas) [*Sars*, 1890, p. 24, as *O. litorea*, pl. 10; *Chevreux* and *Fage*, 1925, p. 274]

Common between tide-marks under stone and amongst weed; Head Ledge to Holywell.

Sub-Order *CAPRELLIDEA*

Family **Caprellidae**

CAPRELLA ACANTHIFERA Leach [*Sars*, 1895, p. 666, pl. 239(3); *Chevreux* and *Fage*, 1925, p. 446]

Among weeds near low-water mark; Holywell.

CAPRELLA LINEARIS (L.) [*Sars*, 1895, p. 657, pl. 236; *Chevreux* and *Fage*, 1925, p. 456]

Fairly common amongst *Tubularia* and *Crisia*; Head Ledge.

Order *DECAPODA*

Sub-Order *NATANTIA*

Tribe *Caridea*

Family **Hippolytidae**

HIPPOLYTE VARIANS Leach [*Kemp*, 1910, p. 100]

Common amongst weeds everywhere.

Family **Alpheidae**

ATHANAS NITESCENS (Leach) [*Kemp*, 1910, p. 122]
Common among corrallines and weed in mid-tidal rock-pools; Head Ledge to Holywell.

Family **Palaemonidae**

PALAEMON SERRATUS (Pennant) [*Kemp*, 1910, p. 130, as *Leander*; *Holthuis*, 1950, p. 57]
Common everywhere among weeds.

PALAEMON ELEGANS Rathke [*Kemp*, 1910, p. 132, as *Leander squilla; Holthuis*, 1950, p. 55]
Fairly common between tide-marks; Head Ledge to Holywell.

Family **Crangonidae**

CRANGON VULGARIS Linnaeus [*Kemp*, 1910, p. 137]
Common everywhere, especially in the deeper water between the Reefs where it is sandy.

Sub-Order *REPTANTIA*

Tribe *Astacura*

Family **Nephropsidae**

HOMARUS GAMMARUS (Linnaeus) [*Holthius*, 1950, p. 99; *Selbie*, 1914, p. 53 as *H. vulgaris* H. M. Edw.]
Occasional specimen found among rocks between tide-marks; Head Ledge to Holywell.

Tribe *Anomura*

Family **Galatheidae**

GALATHEA INTERMEDIA Liljeborg [*Selbie*, 1914, p. 66; *Holthius*, 1950, p. 121]
Several specimens on Outer Reef.

GALATHEA SQUAMIFERA Leach [*Selbie*, 1914, p. 69; *Bull*, 1937, pl. 3, 4; *Holthius*, 1950, p. 118]
Occasionally found under stones near low-water mark; Holywell.

Family **Porcellanidae**

PORCELLANA PLATYCHELES (Pennant) [*Selbie*, 1914, p. 87; *Holthius*, 1950, p. 128]
Common under stones between tide-marks; Head Ledge to Holywell.

PORCELLANA LONGICORNIS (L.) [*Selbie*, 1914, p. 87; *Holthius*, 1950, p. 125]
Fairly common everywhere under stones.

Tribe *Paguridea*

Family **Paguridae**

PAGURUS BERNHARDUS (L.) [*Holthius*, 1950, p. 133; *Selbie*, 1921, p. 15 as *Eupagurus*].

Fairly common between tide-marks, particularly in sandy gravel areas; Head Ledge to Holywell.

PAGURUS PRIDEAUXI (Leach) [*Selbie*, 1921, p. 34 as *Eupagurus*]

Fairly common in sandy areas between tide-marks; Head Ledge to Holywell.

Tribe *Brachyura*

Family **Cancridae**

CANCER PAGURUS L. [*Bell*, 1853, p. 59; *Bouvier*, 1940, p. 224]

Small specimens common under stones and in rock-pools of the intertidal zone, larger specimens occur in the area of the Reefs; Head Ledge to Holywell.

Family **Portunidae**

MACROPIPUS PUBER (L.) [*Palmer*, 1927, p. 882]

Common among rocks near low-water mark; Head Ledge to Holywell.

MACROPIPUS MARMOREUS Leach [*Palmer*, 1927, p. 888]

One specimen only from the Outer Reef.

MACROPIPUS DEPURATOR (L.) [*Palmer*, 1927, p. 893]

Occasionally found to seaward of the Outer Reef.

CARCINUS MAENAS (L.) [*Bell*, 1853, p. 76; *Bouvier*, 1940, p. 234]

Common everywhere between tide-marks.

Family **Xanthidae**

XANTHO INCISUS Leach [*Bouvier*, 1940, p. 265, as *X. floridus*; *Drach* and *Forest*, 1953, p. 11, as *X. floridus*]

A single specimen in a crevice on Head Ledge.

PILUMNUS HIRTELLUS (L.) [*Bell*, 1853, p. 68; *Bouvier*, 1940, p. 255]

Moderately common under stones near low-water mark; Head Ledge to Holywell.

Family **Pinnotheridae**

PINNOTHERES PISUM (Pennant) [*Bell*, 1853, p. 121; *Bouvier*, 1940, p. 301]

Common in mussels; Holywell.

Family **Maiidae**

INACHUS DORYNCHUS Leach [*Bell*, 1853, p. 16; *Bouvier*, 1940, p. 355; *Monod*, 1956, p. 531, as *I. phalangium*]

Two specimens from the seaward side of the Outer Reef.

HYAS COARCTATUS Leach [*Bell*, 1853, p. 35; *Bouvier*, 1940, p. 335]

Single specimen in a rock-pool near low-water mark; Holywell.

MACROPODIA ROSTRATAS (L.) [*Bell*, 1853, p. 2, as *Stenorynchus phalangium*; *Bouvier*, 1940, p. 362]

Several specimens under stones near low-water mark; Holywell.

BIBLIOGRAPHY

BELL, T. (1853). *A history of the British Stalk-Eyed Crustacea.* 386 pp. London.

BOUVIER, E. L. (1940). Decapodes Marcheurs. *Faune Fr.* No. 37, 1.

BULL, H. O. (1937). Notes on the British species of the genus *Galathea*. *Rep. Dove mar. Lab.* (3) No. 4, 38.

CHEVREUX, E. and FAGE, L. (1925). Amphipodes. *Faune Fr.* No. 9, 1.

DARWIN, C. (1851–54). *A monograph of the sub-class Cirripedia.* **1,** (1851); **2,** (1854). London: Ray Society.

DRACH, P. and FOREST, J. (1953). Description et rèpartition des *Xantho* des mers d'Europe. *Arch. Zool. exp. gén.* **90,** 1.

HOLTHUIS, L. B. (1950). Decapoda (K IX)—A. Natantia, Macrura, Reptantia, Anomura—en Stomatopoda (K X). *Fauna Nederl.* Afl. 15, 1.

KEMP, S. (1910). The Decapoda Natantia of the coasts of Ireland. *Sci. Invest. Fish. Br. Ire.* 1908 [1910], No. 1, 1.

KRÜGER, P. (1927). Cirripedia. *Tierw. N.-u. Ostsee,* Teil 10, d, 1, (Lief. 8).

MONOD, T. (1956). Hippidea et Brachyura ouest-africains. *Mém. Inst. franç. d'Afrique Noire* No. 45, 1.

NAYLOR, E. (1955). The comparative external morphology and revised taxonomy of the British species of *Idotea*. *J. mar. biol. Ass. U.K.* **34,** 467.

OMER-COOPER, J. and RAWSON, J. H. 1934. Notes on the British Sphaeromatidea (Crustacea Isopoda). *Rep. Dove Mar. Lab.* (3) No. 2, 22.

PALMER, R. (1927). A revision of the genus *Portunus* (A. Milne-Edwards, Bell, etc.). *J. mar. biol. Ass. U.K.* **14,** 877.

SARS, G. O. (1890). Amphipoda. *An account of the Crustacea of Norway* **1,** 1.

SARS, G. O. (1896). Phyllocarida og Phyllopoda. *Fauna Norvegiae* **1,** 1.

SARS, G. O. (1896–9). Isopoda. *An account of the Crustacea of Norway* **2,** 1.

SARS, G. O. (1901–3). Copepoda, Calanoida. *An account of the Crustacea of Norway* **4,** 1.

SARS, G. O. (1913–18). Cyclopoida. *An account of the Crustacea of Norway* **6,** 1.

SELBIE, C. M. (1914). The Decapoda Reptantia of the coasts of Ireland. Part I. Palinura, Astacura and Anomura (except Paguridea). *Sci. Invest. Fish. Br. Ire.* 1914 No. 1, 1.

SELBIE, C. M. (1921). The Decapoda Reptantia of the coasts of Ireland, Part 2. Paguridea. *Sci. Invest. Fish. Br. Ire.* 1921 No. 1, 1.

SEXTON, E. W. (1942). The relation of *Gammarus zaddachi* Sexton to some other species of *Gammarus* occurring in fresh, estuarine and marine waters. *J. mar. biol. Ass. U.K.* **25,** 575.

SEXTON, E. W. and SPOONER, G. M. (1940). An account of *Marinogammarus* (Schellenberg) gen. nov. Amphipoda, with a description of a new species, *M. pirloti*. *J. mar. biol. Ass. U.K.* **24,** 633.

VAN BENEDEN, P. J. (1861). Crustaces. In: *Recherches sur la fauna littoral de Belgique* 11.

Sub-Phylum **INSECTA**

Class APTERYGOTA

Order *COLLEMBOLA*

Family **Neanuridae**

ANURIDA MARITIMA Laboulbène [*Lubbock*, 1873, p. 193; *Imms*, 1906] (= *Lipura*)

On the surface of rock-pools at and above high-water mark; Head Ledge to Holywell.

Order *THYSANURA*

Family **Machilidae**

PETROBIUS MARITIMUS (Leach) [*Carpenter*, 1913, p. 2; *Womersley*, 1930, p. 393]

Common among rocks above high-water mark; Head Ledge to Holywell.

BIBLIOGRAPHY

CARPENTER, G. H. (1913). Clare Island Survey. Apterygota. *Proc. R. Irish. Acad.* **31**, Part 32, 1.

IMMS, A. D. (1906). Anurida. *L.M.B.C. Memoirs*, No. 13.

LUBBOCK, SIR J. (1873). *Monograph of the Collombola and Thysanura*. 265 pp. London: Ray Society.

WOMERSLEY, H. (1906). Contributions to a study of the British species of Machilidae. *Ann. Mag. nat. Hist.* (10), **5**, 217.

Phylum **MOLLUSCA**

Class POLYPLACOPHORA (- LORICATA)

Family **Lepidochitonidae**

TONICELLA RUBRA (L.) [*Forbes* and *Hanley*, 1849, **2**, p. 399, as *Chiton ruber; Matthews*, 1953, p. 246]

Occasionally found between tide-marks; Head Ledge to Holywell.

LEPIDOCHITONA CINEREA (L.) [*Forbes* and *Hanley*, 1849, **2**, p. 402; *Matthews*, 1953, p. 246]

Moderately common under stones from mid-tide mark to low-tide; Head Ledge to Holywell.

CALLOCHITON ACHATINUS (Brown) [*Jeffreys*, 1865, **3**, p. 226, as *Chiton laevis; Matthews*, 1953, p. 246]

Occasionally found on the Reefs.

Family **Cryptoplacidae**

ACANTHOCHITONA CRINATA (Pennant) [*Forbes* and *Hanley*, 1849, **2**, p. 393, as *Chiton fascicularis; Matthews*, 1953, p. 246]

Fairly common between tide-marks; Head Ledge to Holywell.

Class GASTROPODA

Sub-Class PROSOBRANCHIA

Order *ARCHAEOGASTROPODA*

Family **Patellidae**

PATELLA VULGATA L. [*Jeffreys*, 1865, **3**, p. 236]

Abundant on rocks everywhere between tide-marks.

PATELLA ASPERA Lamarck (= PATELLA ATHLETICA Bean) [*Jeffreys*, 1865, **3**, p. 237, as var *depressa*]

Occurs occasionally with *P. vulgata*.

PATELLA INTERMEDIA Jeffreys (= PATELLA DEPRESSA Pennant) [*Jeffreys*, 1865, **3**, p. 237, as var *intermedia*]

Localised on rocks between tide-marks, especially where slightly exposed; Head Ledge.

Family **Trochidae**

CALLIOSTOMA ZIZYPHINUM (L.) [*Forbes* and *Hanley*, 1850, **2**, p. 491, as *Trochus*]

Common under stones and in crevices on Reefs.

CALLIOSTOMA PAPILLOSUM (da Costa) [*Forbes* and *Hanley*, 1850, **2**, p. 499, as *Trochus granulatus*]
Dead shells only near Head Ledge.

CANTHARIDUS MONTAGUI (W. Wood) [*Jeffreys*, 1865, **2**, p. 320, as *Trochus*]
One specimen from the Outer Reef.

GIBBULA CINERARIA (L.) [*Forbes* and *Hanley*, 1850, **2**, p. 516, as *Trochus*]
Common everywhere between tide-marks.

GIBBULA UMBILICALIS (da Costa) [*Forbes* and *Hanley*, 1850, **2**, p. 519, as *Trochus umbilicatus*]
Occurs with *G. cineraria* extending to higher tidal levels.

Order *MESOGASTROPODA*

Family **Littorinidae**

LITTORINA LITTORALIS (L.) [*Forbes* and *Hanley*, 1850, **3**, p. 45]
Abundant everywhere on *Fucus* and other weeds.

LITTORINA LITTOREA (L.) [*Jeffreys*, 1865, **3**, p. 368]
Fairly common on all grounds between tide-marks.

LITTORINA NERITOIDES (L.) [*Jeffreys*, 1865, **3**, p. 361]
Common on all rocks and in crevices above high-water mark.

LITTORINA SAXATILIS (Olivi) [*Jeffreys*, 1865, **3**, p. 364, as *L. rudis*]
Abundant on all rocks near high-water mark.

Family **Cypraeidae**

TRIVIA ARCTICA (Montagu) [*Lebour*, 1933a, p. 483—*T. europaea* in part, of the Plymouth Marine Fauna, 1931]
Fairly common between the Reefs and at extreme low-water; Holywell.

TRIVIA MONACHA (da Costa) [*Lebour*, 1933a, p. 483]
Occasional specimens between tide-marks; Head Ledge.

Family **Epitoniidae**

CLATHRUS CLATHRUS (L.) [*Jeffreys*, 1867, **4**, p. 91, as *Scalaria communis*]
Several dead shells near Head Ledge.

Order *STENOGLOSSA*

Family **Muricidae**

OCENEBRA ERINACEA (L.) [*Jeffreys*, 1867, **4**, p. 306, as *Murex*]
Moderately common on rocks between tide-marks; Head Ledge to Holywell.

NUCELLA LAPILLUS (L.) [*Jeffreys*, 1867, **4**, p. 276, as *Purpura*]
Moderately common on rocks everywhere, dead shells very common.

Family **Buccinidae**

BUCCINUM UNDATUM L. [*Jeffreys*, 1867, **4**, p. 285]
Dead shells common.

Family **Nassariidae**

NASSARIUS RETICULATUS (L.) [*Forbes* and *Hanley*, 1851, **3**, p. 388, as *Nassa*]
Fairly common near low-water mark and in *Laminaria;* Holywell.

NASSARIUS INCRASSATUS (Ström) [*Forbes* and *Hanley*, 1851, **3**, p. 391, as *Nassa*]
Fairly common in all rocky situations, under stones and in crevices.

Order *APLYSIOMORPHA*

Family **Aplysiidae**

APLYSIA PUNCTATA Cuvier [*Garstang*, 1890, p. 401]
Occasional small specimens on *Laminaria* between the Reefs.

Order *NUDIBRANCHIA*

Sub-Order *DORIDACEA*

Family **Glossodorididae**

ROSTANGA RUFESCENS Iredale and O'Donoghue [*Alder* and *Hancock*, 1855, p. 42, as *Doris coccinea*]
Several small specimens found occasionally on the sponge *Microciona atrasanguinea*; Head Ledge to Holywell.

ARCHIDORIS PSEUDOARGUS (Rapp) [including *britannica* and *flammea*] [Alder and Hancock, 1855, p. 41, as *Doris tuberculata*] (=*A. britannica* and *A. flammea* of the 'Plymouth Fauna List', 1931)
Single large specimen in crevice on Outer Reef.

Sub-Order *ARMINACEA*

Family **Proctonotidae**

JANOLUS HYALINUS (Alder and Hancock) [*Eliot*, 1910, p. 165]
Occasional small specimens in rock-pools between tide-marks; Head Ledge.

Sub-Order *EOLIDACEA*

Family **Aeolidiidae**

AEOLIDIA PAPILLOSA (L.) [*Alder* and *Hancock*, 1855, p. 48, as *Eolis*]
Fairly common among rocks and weed; Head Ledge to Holywell.

Class LAMELLIBRANCHIA (- BIVALVIA)

Order *DYSODONTA*

Family **Mytilidae**

MYTILUS EDULIS L. [*Jeffreys*, 1863, **2**, p. 104]
Common everywhere attached to rocks and to groynes at Holywell.

Order *PSEUDOLAMELLIBRANCHIA*

Family **Pectinidae**

CHLAMYS OPERCULARIS (L.) [*Jeffreys*, 1863, **2**, p. 59, as *Pecten*]
Several small specimens between tide-marks to west of Head Ledge.

CHLAMYS VARIA (L.) [*Jeffreys*, 1863, **2**, p. 53, as *Pecten*]
Dead shells fairly common Head Ledge to Holywell.

Order *EULAMELLIBRANCHIA*

Family **Cardiidae**

CARDIUM EDULE L. [*Forbes* and *Hanley*, 1849, **2**, p. 15]
Dead shells common on all grounds, several specimens in sand to west of Head Ledge.

Family **Veneridae**

VENUS (VENUS) VERRUCOSA L. [*Forbes* and *Hanley*, 1848, **1**, p. 401]
Dead shells only; Holywell.

VENUS (CLAUSINELLA) FASCIATA da Costa [*Forbes* and *Hanley*, 1848, **1**, p. 415]
Several specimens in coarse gravel between tide-marks; Holywell.

VENERUPIS SAXATILIS (Fleuriau) [*Jeffreys*, 1863, **2**, p. 357, as *Tapes pullastra* var. *perforans*]
Several specimens in sandy rock crevices between tide-marks; Head Ledge.

Family **Asaphidae**

GARI DEPRESSA (Pennant) [*Jeffreys*, 1863, **2**, p. 398, as *Psammobia vespertina*]
Several specimens in sand to west of Head Ledge. Dead shells common.

GARI FERVENSIS (Gmelin) [*Jeffreys*, 1863, **2**, p. 396, as *Psammobia ferroensis*]
Several dead shells washed up; Holywell.

GARI TELLINELLA (Lamarck) [*Jeffreys*, 1863, **2**, p. 392, as *Psammobia*]
Several specimens in gravel near low-water mark; Head Ledge.

Family **Mactridae**

SPISULA SOLIDA (L.) [*Forbes* and *Hanley*, 1848, **1**, p. 351 and 354, as *Mactra solida* and *M. truncata*]
Dead shells common; Holywell.

Family **Tellinidae**

TELLINA FABULA Gmelin [*Forbes* and *Hanley*, 1848, **1**, p. 302]
Occasional specimens in silty sand near low-water mark; Head Ledge to Holywell.

Family **Solenidae**

ENSIS SILIQUA (L.) [*Jeffreys*, 1865, **3**, p. 18, as *Solen*: *Holme*, 1951, p. 639]
Occasional specimens mid-tidal zone in sandy areas; Holywell.

Family **Hiatellidae**

HIATELLA STRIATA (Fleuriau) [*Forbes* and *Hanley*, 1848, **1**, p. 146, as *Saxicava rugosa*]
Boring in Greensand, Chalk and Gault between tide-marks; Head Ledge to Holywell.

Family **Pholadidae**

PHOLAS DACTYLUS L. [*Forbes* and *Hanley*, 1848, **1**, p. 108]
Abundant boring in Gault and Greensand between tide-marks; Head Ledge to Holywell.

BARNEA PARVA (Pennant) [*Forbes* and *Hanley*, 1848, **1**, p. 111, as *Pholas*]
In same localities as *Pholas dactylus*.

Class CEPHALOPODA

Order *DECAPODA*

Family **Sepiidae**

SEPIA OFFICINALIS (L.) [*Tompsett*, 1939, p. 1]
Spawn found in rock-pools between tide-marks, late July; Holywell.

BIBLIOGRAPHY

ALDER, J. and HANCOCK, A. (1845–55). *A monograph of the British Nudibranchiate Mollusca.* 369 pp. London: Ray Society.

ELIOT, C. (1910). *A monograph of the British Nudibranchiate Mollusca; with figures of the species.* Part 8 (Supplementary). 198 pp. London: Ray Society.

FORBES, E. and HANLEY, S. (1848–53). *A history of the British Mollusca, and their shells.* London, 4 volumes, 51 plates. **1**, pp. 1–486 (1848); **2**, pp. 1–480 (1849); pp. 481–557 (1850); **3**, pp. 1–320 (1850); pp. 321–616 (1851); **4**, pp. 1–280 (1852); pp. 281–301 (1853). [Full details of parts in *J. Conch.*, 20, 150.]

GARSTANG, W. (1890). A complete list of the Opisthobranchiate Mollusca found at Plymouth. *J. mar. biol. Ass. U.K.*, **1**, 399.

HOLME, N. J. (1951). The identification of British species of the genus *Ensis* Schumacher (Lamellibranchiata). *J. mar. biol. Ass. U.K.* **32**, 1.

JEFFREYS, J. G. (1863–69). *British conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas.* Vol. 2–5, **2** (1863), 465 pp.; **3** (1865), 393 pp.; **4** (1867), 486 pp.; **5** (1869), 258 pp. London.

LEBOUR, M. V. (1933). The British species of Trivia: *T. arctica* and *T. monacha*. *J. mar. biol. Ass. U.K.* **18**, 123.

MATTHEWS, G. (1953). A key for use in the identification of British chitons. *Proc. malacol. Soc. Lond* **29**, 241.

TOMPSETT, D. H. (1939). Sepia. *Liverpool mar. biol. Comm.* Memoir **18**, 184 pp.

Phylum **POLYZOA** s. str.

Order *CYCLOSTOMATA*

Family **Crisiidae**

CRISIA ACULEATA Hassall [*Harmer*, 1891, p. 132]
Near low-tide mark on weeds stones etc.; Head Ledge to Holywell.

CRISIA DENTICULATA (Lamarck) [*Harmer*, 1891, p. 129]
Not uncommon on weeds on the Outer Reef.

CRISIDIA CORNUTA (L.) [*Hincks*, 1880, p. 419, as *Crisia*]
Common on rocks and weeds between tide-marks; Head Ledge to Holywell.

Order *GYMNOLAEMATA*

Sub-Order *CHEILOSTOMATA*

Family **Membraniporidae**

MEMBRANIPORA MEMBRANACEA (L.) [*Hincks*, 1880, p. 140]
On *Fucus* and *Laminaria*; Head Ledge to Holywell.

Family **Flustridae**

FLUSTRA FOLIACEA [*Hincks*, 1880, p. 115]
Common on jetsam in rock-pools between tide-marks.

Family **Bicellariellidae**

BUGULA AVICULARIA (L.) [*Hincks*, 1880, p. 75]
Occasionally on the Outer Reef.
BUGULA PLUMOSA (Pallas) [*Hincks*, 1880, p. 84]
Fairly common between tide-marks; Head Ledge to Holywell.

Family **Umbonulidae**

UMBONULA LITTORALIS Hastings, 1944, p. 280 [*Allen* and *Todd*, 1900, p. 204, as *U. verrucosa*]
Common on rocks between tide-marks; Head Ledge to Holywell.

Sub-Order *CTENOSTOMATA*

Family **Alcyonidiidae**

ALCYONIDIUM GELATINOSUM (L.) [*Hincks*, 1880, p. 491]
Several specimens in the jetsam of mid-tidal rock-pools.

Family **Flustrellidae**

FLUSTRELLA HISPIDA (Fabricius) [*Hincks*, 1880, p. 506]
Common everywhere on weeds between tide-marks.

Phylum **KAMPTOZOA (POLYZOA ENTOPROCTA)**

Family **Pedicellinidae**

PEDICELLINA CERNUA (Pallas) [*Hincks*, 1880, p. 565]
Fairly common near low-water mark everywhere.

BIBLIOGRAPHY

ALLEN, E. J. and TODD, R. A. (1900). The fauna of the Salcombe Estuary. *J. mar. biol. Ass. U.K.* **6**, 151.
HARMER, S. F. (1891). On the British species of *Crisia*. *Quart. J. micr. Sci.* **32**, 127.
HASTINGS, A. B. (1944). Notes on the Polyzoa (Bryozoa). I. *Umbonula verrucosa* auctt.: *U. ovicellata*, sp. n. and *U. littoralis*, sp. n. *Ann. Mag. nat. Hist.* (11) **11**, 273.
HINCKS, T. (1880). *A history of the British marine Polyzoa* **1**, 1.

Phylum **ECHINODERMATA**

Class ASTEROIDEA

Order *SPINULOSA*

Family **Asterinidae**

ASTERINA GIBBOSA (Pennant) [*Mortensen*, 1927, p. 98]
Several specimens under stones between tide-marks; Head Ledge to Holywell.

Family **Solasteridae**

SOLASTER (CROSSASTER) PAPPOSUS (L.) [*Mortensen*, 1927, p. 112]
One specimen between tide-marks; Holywell.

Order *FORCIPULATA*

Family **Asteriidae**

ASTERIAS RUBENS L. [*Mortensen*, 1927, 139]
Occasionally found below tide-marks.

Class OPHIUROIDEA

Order *OPHIURAE*

Family **Ophiotrichidae**

OPHIOTHRIX FRAGILIS (Abildgaard) [*Mortensen*, 1927, p. 174]
Small specimens common under stones and in rock-pools between tide-marks; Head Ledge to Holywell.

Family **Ophiocomidae**

OPHIOCOMINA NIGRA (Abildgaard) [*Mortensen*, 1927, p. 178]
Found in association with *Ophiothrix fragilis* but not so abundant.

Class ECHINOIDEA

Order *DIADEMATOIDEA*

Family **Echinidae**

PSAMMECHINUS MILIARIS (Gmelin) [*Mortensen*, 1927, p. 294]
Occasionally found under stones near low-water mark and in rock-pools. All specimens obtained were small; Head Ledge to Holywell.

BIBLIOGRAPHY

MORTENSEN, T. (1927). *Handbook of the echinoderms of the British Isles.* 471 pp. Oxford.

Phylum **CHORDATA**

Sub-Phylum **TUNICATA**

Class ASCIDIACEA

Order *PLEUROGONA*

Sub-order *STOLIDOBRANCHIATA*

Family **Molgulidae**

MOLGULA OCULATA Forbes [*Berrill*, 1950, p. 252]
Common in areas of clean fine gravel; Head Ledge.

Family **Styelidae**

DENDRODOA GROSSULARIA (Van Beneden) [*Berrill*, 1950, p. 198]
Abundant on rocks between tide-marks; Head Ledge to Holywell.

Sub-family Botryllinae

BOTRYLLUS SCHLOSSERI (Pallas) [*Berrill*, 1950, p. 216]
Fairly common on rocks particularly the Reefs; Head Ledge to Holywell.

Order *ENTEROGONA*

Sub-order *APLOUSOBRANCHIATA*

Family **Polyclinidae** (- Synoicidae)

MORCHELLIUM ARGUS (Milne-Edwards) [*Berrill*, 1950, p. 95]
Common on rocks between tide-marks; Head Ledge to Holywell.

BIBLIOGRAPHY

BERRILL, N. J. (1950). *The Tunicata, with an account of the British species.* 354 pp. London: Ray Society.

Sub-Phylum **VERTEBRATA**

Class SELACHII

Order *PLEUROTREMATA*

Family **Scyliorhinidae**

SCYLIORHINUS CANICULUS (L.) [*Day*, **2**, 1880-4, p. 309, Pl. 159, 2, as *Scyllium*; Int. Coun. 10]
Occasional small specimens caught in inter-tidal rock-pools. Holywell. Often caught offshore by fishing vessels.

Class PISCES

Sub-class NEOPTERYGII

Order *APODES*

Family **Congridae**

CONGER CONGER (L.) [*Day*, 1880-4, **2**, p. 250, Pl. 142, 2, as *C. vulgaris*; Int. Coun. 134] ' Conger Eel '
Fairly common inshore.

Order *SOLENICHTHYES*

Family **Syngnathidae**

NEROPHIS LUMBRICIFORMIS Pennant [*Day*, 1880-4, **2**, p. 263, Pl. 144, 6; Int. Coun. 151] ' Worm Pipe-Fish '
Common under stones between tide-marks; Head Ledge to Holywell.

Order *ANACANTHINI*

Family **Gadidae**

CILIATA MUSTELA (L.) [*Svetovidov*, 1948, 9, Pt. 4, p. 90; *Day*, 1880-4, p. 314, Pl. 89, 2, as *Motella*; Int. Coun. 189] ' Five-bearded Rockling '
Common inshore: inter-tidal rock-pools near low-water mark; Head Ledge to Holywell.

GAIDROPSARUS MEDITERRANEUS (L.) [*Svetovidov*, 1948, 9, Pt. 4, p. 82, Pl. 1, 2] ' Three-bearded Rockling '

Fairly common in rock-pools at extreme low tide; Head Ledge to Holywell.

Order *PERCOMORPHI*

Family **Gobiidae**

GOBIUS NIGER L. [*Holt* and *Byrne*, 1901, p. 43, f. 1; *Lebour*, 1919, p. 74, Pl. 4, 24; *Petersen*, 1917, Pl. 1, 6; Int. Coun. 292] ' Black Goby '

Occasional specimens in inter-tidal rock-pools; Holywell.

GOBIUS PAGANELLUS L. [*Holt* and *Byrne*, 1901, p. 45, Pl. 1, 1 and 2; *Lebour*, 1919, p. 71, Pl. 4, 23; Int. Coun. 293] ' Rock Goby '

Common between tide-marks; Head Ledge to Holywell.

GOBIUS FLAVESCENS Fabricius [*Holt* and *Byrne*, 1901, p. 49, f. 2, as *G. ruthensparri* Euphrasèn; *Lebour*, 1919, p. 69, Pl. 3, 14; *Petersen*, 1917, Pl. 1, 18; Int. Coun. 295] ' Spotted Goby '

Several specimens in rock-pools near low-tide mark; Head Ledge to Holywell.

GOBIUS MINUTUS Pallas [*Holt* and *Byrne*, 1901, p. 50; *Lebour*, 1919, p. 55, Pl. 1, 1; *Petersen*, 1919, Pl. 3, 2; Int. Coun. 297] ' Common Goby '; ' Sand Goby '

Several specimens netted to west of Head Ledge at extreme low-water.

Family **Blenniidae**

BLENNIUS PHOLIS L. [*Day*, 1880-4, **1**, p. 203, Pl. 60, 2, Int. Coun. 309] ' Common Blenny '; ' Shanny '

Common between tide-marks in all areas.

BLENNIUS OCELLARIS L. [*Day*, 1880-4, **1**, p. 201, Pl. 59, 2; Int. Coun. 308] ' Butterfly Blenny '

Fairly common at extreme low-water; Head Ledge to Holywell.

BLENNIUS GATTORUGINE L. [*Day*, 1880-4, **1**, p. 198, Pl. 59, 1; Int. Coun. 306] ' Tompot Blenny '

Fairly common among rocks; Head Ledge to Holywell.

Order *HETEROSOMATA*

Family **Pleuronectidae**

PLEURONECTES PLATESSA L. [*Day*, 1880-4, **2**, p. 25, Pl. 101; Int. Coun. 390] ' Plaice '

Small specimens occasionally found in sand and under rocks in inter-tidal rock-pools; Head Ledge.

Order *XENOPTERYGII*

Family **Gobiesocidae**

LEPADOGASTER LEPADOGASTER (Bonnaterre) [*Day*, 1880-4, **1**, p. 189, Pl. 57, 1 as *L. gouanii*; Int. Coun. 409] ' Cornish Sucker '

Fairly common between tide-marks; Head Ledge to Holywell.

Order *SCLEROPAREI*

Family **Cottidae**

COTTUS SCORPIUS L. [*Day*, 1880-4, **1**, p. 49, Pl. 20, 1; Int. Coun. 358] 'Sea Scorpion'

Several specimens between Reefs.

COTTUS BUBALIS Euphrasen [*Day*, 1880-4, **1**, p. 51, Pl. 20, 2; Int. Coun. 359] 'Father Lasher'

Common in rock-pools near low-water mark; Head Ledge to Holywell.

BIBLIOGRAPHY

DAY, F. (1880–84). *The fishes of Great Britain and Ireland.* **1** (1880), 336 pp.; **2** (1884), 388 pp. London.

HOLT, E. W. L. and BYRNE, L. W. (1901). The British and Irish gobies. *Rep. Sea Inl. Fish. Ire., Sci. Invest.*, Appendix III, 37.

LEBOUR, M. V. (1919). The young of the Gobiidae from the neighbourhood of Plymouth. *J. mar. biol. Ass. U.K.* **12**, 48.

PETERSEN, C. G. J. (1917). On the development of our common gobies (*Gobius*) from the egg to the adult stages. *Rep. Danish biol. Sta.* **24**, 3.

SVETOVIDOV, A. N. (1948). Gadiformes. *Fauna Rossii, Fishes*, **9**, Pt. 4, 1. (Zool. Inst. Acad. Sci., Moscow N.S. No. 34) [In Russian].

APPENDIX I

A list of the seaweeds found growing attached between the Wish Tower and the Head Ledge of Beachy Head.

CHLOROPHYCEAE

ULOTRICHALES

Ulvaceae

ENTEROMORPHA Link, 1820.

compressa (L.) Grev.

intestinalis (L.) Link.

ULVA Linnaeus, 1753.

lactuca L. var. *latissima* (L.) D.C.

CLADOPHORALES

Cladophoraceae

CHAETOMORPHA Kützing, 1845.

melagonium (Web. et Mohr) Kütz.

Cladophora Kützing, 1843.

rupestris (L.) Kütz.

CODIALES

Bryopsidaceae

BRYOPSIS Lamouroux, 1809.

plumosa (Huds.) Ag.

PHAEOPHYCEAE

ECTOCARPALES

Ectocarpaceae

ECTOCARPUS Lyngbye, 1819.

confervoides (Roth) Le Jol.

LAMINARIALES
Laminariaceae
LAMINARIA Lamouroux, 1813.
digitata (Huds.) Lamour.
saccharina (L.) Lamour.
SPHACELARIALES
Cladostephaceae
CLADOSTEPHUS Agardh, 1817.
spongiosus (Huds.) Ag.
DICTYOTALES
Dictyotaceae
DICTYOTA Lamouroux, 1809.
dichotoma (Huds.) Lamour.
FUCALES
Fucaceae
ASCOPHYLLUM Stackhouse, 1809.
nodosum (L.) Le Jol.
FUCUS Linnaeus, 1753.
serratus L.
spiralis L.
vesiculosus L.
PELVETIA Decaisne et Thuret, 1845.
canaliculata (L.) Dcne. et Thur.

RHODOPHYCEAE

BANGIOPHYCIDAE
BANGIALES
Bangiaceae
PORPHYRA Agardh, 1824.
umbilicalis (L.) Kütz.
FLORIDEOPHYCIDAE
NEMALIONALES
Acrochaetiaceae
RHODOCHORTON Nageli, 1861.
floridulum
GELIDIALES
Gelidiaceae
GELIDIUM Lamouroux, 1813.
GIGARTINALES
Rhodophyllidaceae
CALLIBLEPHARIS Kützing, 1843.
**ciliata* (Huds.) Kütz.
CYSTOCLONIUM Kützing, 1843.
purpureum (Huds.) Batt.
Plocamiaceae
PLOCAMIUM Lamouroux, 1813.
coccineum (Huds.) Lyngb.

Gracilariaceae
GRACILARIA Greville, 1830.
verrucosa (Huds.) Papenf.
GIGARTINALES (contd.)
Phyllophoraceae
PHYLLOPHORA Greville, 1830.
**rubens* (L.) Grev.
Gigartinaceae
CHONDRUS Stackhouse, 1797.
crispus (L.) Stackh.
CRYPTONEMIALES
Corallinaceae
CORALLINA Linnaeus emend. Lambouroux, 1812.
officinalis L.
RHODYMENIALES
Rhodymeniaceae
RHODYMENIA Greville, 1830.
**palmata* (L.) Grev.
**pseudopalmata* (Lamour.) Silva
CERAMIALES
Ceramiaceae
CERAMIUM Roth, 1797.
rubrum (Huds.) Ag.
GRIFFITHSIA Agardh, 1817.
fluosculosa (Ellis) Batt.
Rhodomelaceae
LAURENCIA Lamouroux, 1813.
pinnatifida (Huds.) Lamour.
Rhodomelaceae (contd.)
POLYSIPHONIA Greville, 1824.
nigrescens (Sm.) Grev.

This classification is that used by Mary Parke in her Check-list of British Marine Algae, *J. mar. biol. Ass. U.K.* **32**, 497.

Species marked thus * were found in the jetsom only, in all probability they are to be found attached outside the Reefs.

A NEW SPECIES AND GENUS OF KRAUSSINIDAE (BRACHIOPODA) WITH A NOTE ON FEEDING

BY

D. ATKINS, D.Sc.

From the Marine Biological Laboratory, Plymouth

[Accepted 11th March 1958]

(With 1 plate and 14 figures in the text)

CONTENTS

	Page
Introduction	559
Pumilus gen. nov.	560
Pumilus antiquatus sp. nov.	560
Diagnostic description	560
Notes on the structure :	
The musculature	564
The mantle sinuses	564
The digestive system	565
The gonads and nephridia	567
The lophophore	572
The structure of the adult lophophore	572
Growth stages of the lophophore	575
The ciliary feeding mechanism	576
The ciliation of the lophophore and of the mantle	576
The ciliary currents	577
Discussion and affinities	578
Acknowledgments	580
Summary	580
References	580
Explanation of the plate	581

INTRODUCTION

Specimens of what proved to be a new species and genus of brachiopod from Lyttelton, New Zealand, were first noticed in January 1956, thirteen of shell-length 1·27 to 4·35 mm. being found among *Terebratella inconspicua* (Sowerby) and *Tegulorhynchia nigricans* (Sowerby) attached to rock sent to me by Professor E. Percival of Christchurch, New Zealand. Three, two old shells and one recently dead were entangled in the byssal nest of a *Modiolaria impacta* (Hermann),* and had byssal threads attached to them : this had probably caused the death of the two.

It would seem to be a common species at Lyttelton, for a further fifty-three specimens were taken from a stone approximately $6 \times 4 \times 3$ inches received from Professor Percival in July 1957. The largest individual had a shell length of 4·7 mm. and width of 3·4 mm. and has been chosen as a syntype (Pl. 1, figs. A1, A2, and Fig. 14). Some fourteen preserved individuals were attached to the shell of a *Tegulorhynchia nigricans* sent to me by Mr G. Owen :

* Kindly identified by Dr J. Morton.

the largest had a shell length of 3·8 mm. and width of 3·2 mm. He also allowed me to examine some material of *Terebratella* dated 30th March, 1941 given to him by Professor Percival : amongst this were thirty-six examples of the new species of shell length 1 to 3·55 mm. Altogether over a hundred specimens have now been seen, the largest with a shell length of 4·7 mm. It is apparently a small and inconspicuous species, so that it is very understandable that it has remained undiscovered for so long, possibly being mistaken for the young of *Terebratella inconspicua*. As it occurs amongst these it would seem to have the same habitat as Percival (1944) described for *Terebratella* at Lyttelton, New Zealand : on the shore up to about half tide mark.

The new species at about 4 mm. shell length has a generally aged appearance, with well-marked growth lines. It has been named *Pumilus antiquatus* with reference to its small size and its general appearance.

In this paper the pedicle valve is regarded as ventral and the brachial as dorsal, as they were previously to 1944. In that year Percival concluded from his work on the embryology of *Terebratella inconspicua* (Sowerby) that dorsal and ventral should be reversed, but later (1953) from his study of the embryology of *Tegulorhynchia nigricans* (Sowerby) reached the conclusion that the old orientation was after all the correct one.

All figures have been drawn with the aid of a camera lucida.

PUMILUS gen. nov.

Small kraussinid brachiopod with adult lophophore schizolophous, brachial skeleton like that of immature *Kraussina*.

PUMILUS ANTIQUATUS sp. nov.

Diagnostic description

The shell is small, up to 4·7 mm. long, elongated triangular, with fairly short, nearly straight hinge line : it is strongly sulcate at some 2·6 mm. shell

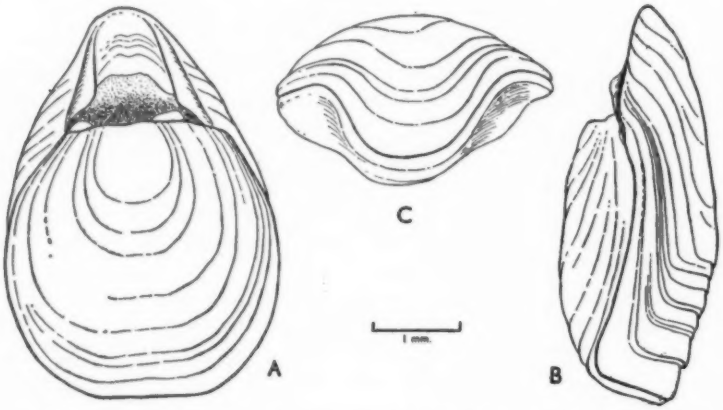


Fig. 1.—*Pumilus antiquatus*, shell length 4·4 mm. and width 3·1 mm. A. Brachial ; B. Lateral ; C. anterior view, with brachial valve above.

length upwards. Some variation in shape occurs, a number of individuals being broader and less deeply sulcate than others (Pl. 1, figs. B1, B2) ; the two variations are illustrated by the syntypes in Plate 1. A paratype (length 4·4 mm.) of the same shape as syntype A is shown in brachial, frontal and side view in Fig. 1. The test is smooth with strongly marked growth lines, and is conspicuously punctate. The beak is long and sub-erect : the foramen large, triangular and incomplete : the deltidial plates narrow and disjunct : the pedicle collar well developed. The foramen shows some variation in shape, no doubt depending on the length of the pedicle and the position of the animal with regard to the surface of attachment, a short pedicle resulting in abrasion of the apex of the beak. Examples of this variation are shown

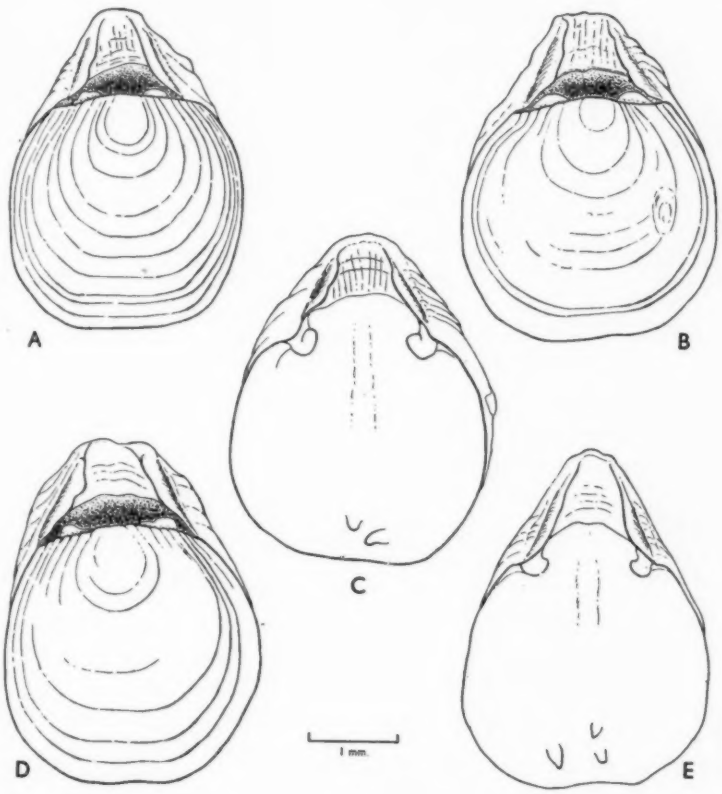


Fig. 2.—*Pumilus antiquatus*, to show variation in the shape of the foramen.

A. Shell length 3·6 mm. and width 2·65 mm.

B. Shell length 3·65 mm. and width 2·9 mm.

C. Interior of pedicle valve of another specimen of the same size as that shown in B.

D. Shell length 3·9 mm. and width 2·9 mm., with apex of beak worn.

E. Interior of pedicle valve of a specimen of shell length 3·9 mm. and width 2·7 mm. with beak unworn.

in Fig. 2. The hinge teeth are without dental plates. The pedicle valve has a slight median elevation dying out toward the middle of the valve; submarginal tubercles are absent or one to five at the anterior margin (Fig. 2 C, E).

The socket ridges are prominent; the distal socket ridges project behind the cardinal border (Figs. 1, 2, 3). In adults a strong ridge runs transversely inwards from the inner surface of the inner socket ridge (Fig. 3 D). A cardinal process is lacking. There is no loop. A low median septum extends over approximately the middle third of the brachial valve and ends anteriorly in a slight rounded protuberance. Somewhat posterior to the middle of the septum arise two low divergent lamellae, which may be approximately

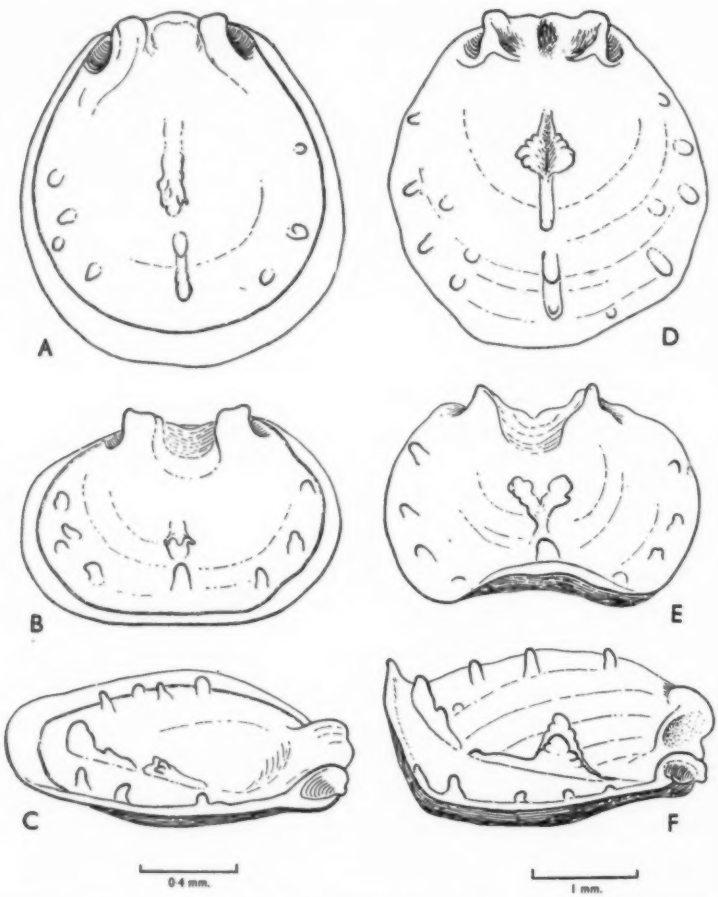


Fig. 3.—*Pumilus antiquatus*. Brachial valves of: A–C individual 1·8 mm. long and 1·3 mm. wide; D–F individual 4·0 mm. long and 3·0 mm. wide. A and D, interior; B and E, anterior; C and F, lateral views.

triangular with tuberculated extremities (Fig. 3, D–F), or occasionally rectangular. The position of the lamellae with regard to the septum shifts with growth : in the immature shell they arise more anteriorly (Fig. 3 C). These divergent plates support the sides of the median invagination of the lophophore in the young, and in the adult fit into its posterior end (Fig. 9, p. 572). One or two tooth-like tubercles continue the line of the median septum, although separated from it. A number of submarginal tubercles are present (Fig. 3). The median tubercles appear early, before the septum, and this allows of the easy identification of specimens of some 1 mm. shell length, which might otherwise be confused with the young of *Terebratella inconspicua* with which they occur.

The smallest specimen with intact shell had a length of 1·27 mm. (Fig. 4 A, B). An exceedingly low ridge represented the septum. Two

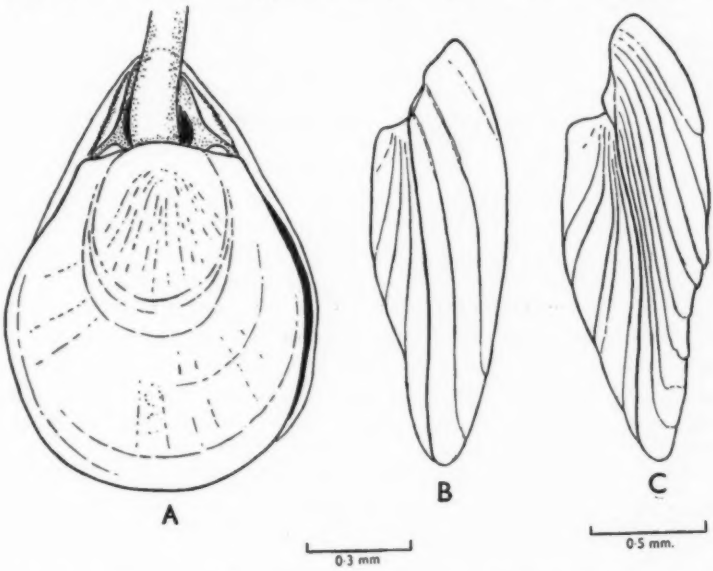


Fig. 4.—*Pumilus antiquatus*. A. brachial ; B. lateral view of individual 1·27 mm. long and 0·9 mm. wide. C. lateral view of specimen 1·95 mm. shell length.
In A two median tubercles are indicated by broken outlines.

median tubercles were present anteriorly with a sub-marginal one on each side. The latter were too inconspicuous to be visible through the brachial valve and are not indicated in the figure. At this stage the shell is without sulcation : at a shell length of 1·95 mm. sulcation is slight (Fig. 4 C).

The colour of the shell is whitish, but most specimens were coated, to a greater or lesser degree, with a dark brown deposit, making the growth lines especially prominent and giving to individuals an ancient look.

The mantle margin bears setae, especially long anteriorly and antero-laterally (Fig. 14, p. 577) : these, however, are easily lost in handling, and have been omitted from most of the figures.

The lophophore is schizolophous, of the large based terebratellacean type, set low on the dorsal mantle : it is supported by the divergent lamellae and by spicules, which, however, are absent from the filaments. The filaments are in a double alternating series, except for some twenty in single series behind the mouth. Spicules are not present in the body wall or mantle in the material examined.

The diductor muscles are inserted on the pedicle valve behind the adductors : the posterior adductors are composed of striated fibres.

The gonad is hermaphrodite.

Type specimens

The syntypes and one paratype have been deposited in the British Museum (Natural History). The syntypes have been given the numbers ZB.1620 (syntype A) ZB. 1621 (syntype B) and the paratype depicted in Fig. 1 the number ZB.1622. The remainder of the material will be held by me for the present.

NOTES ON THE STRUCTURE

The musculature

The adductor muscles pass almost directly across the shell cavity (Fig. 5). The tendons of the right and left adductors remain separate for much of their length, uniting a short distance from their attachment to the pedicle valve (Fig. 7 B). The posterior adductors are most clearly striated.

The diductor muscles are inserted on the pedicle valve behind the adductors as in *Megerlia* (Fischer & Œhlert, 1891, pl. vii, fig. 11 t), and as in *Argyrotheca* and *Megathyris* (Thomson, 1927, pp. 210 & 214) : they pass almost directly across the shell cavity. The insertions on the pedicle valve are quite extensive. The tendons unite dorsally and are inserted transversely at the edge of the dorsal umbo ; a cardinal process is wanting. The diductors of *Pumilus antiquatus* seem to agree in position and direction with the accessory diductors of such forms as *Magellania flavesceus* and *Macandrevia cranium* as shown in the figures of Thomson (1927, fig. 8) and Fischer & Œhlert (1891, pl. v, fig. 10).

The dorsal pedicle muscles are inserted to the inner side of the inner socket ridges, which in adults have a ridge running inwards from their inner surfaces, marking the anterior limit of attachment of the muscles. Their insertion is behind that of the adductors. Each ventral pedicle muscle has a large insertion on the pedicle valve situated to the outside of the adductor insertion and extending anteriorly and posteriorly to it.

The mantle sinuses

In the brachial valve the coelomic or visceral cavity extends to the anterior edge of the lophophore. It is divided by mesentery (Fig. 7 ; 6 C), by septum and divergent lamellae (Fig. 6 B) and by a broad band of connective tissue (Fig. 6 A), one following the other postero-anteriorly. On each side of the mid line each half is continued anteriorly as a mantle sinus.

In the pedicle valve a single pair of mantle sinuses in the mid region continue the two halves of the coelomic cavity anteriorly (Fig. 6 C, B). There is thus a single pair of main trunks in each mantle lobe in *Pumilus antiquatus*.

The finer branches of the mantle sinuses were not investigated.

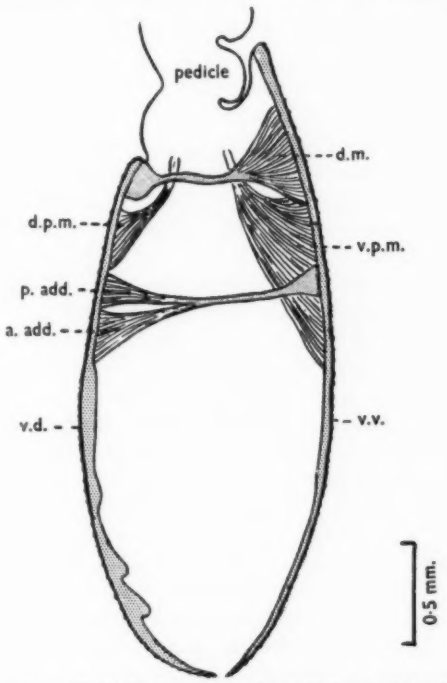


Fig. 5.—*Pumilus antiquatus*. Optical section of a decalcified and stained specimen to show the muscles : somewhat diagrammatic. *a. add.*, anterior and *p. add.*, posterior adductors ; *d.m.*, diductor muscle ; *d.p.m.*, dorsal and *v.p.m.*, ventral pedicle muscles ; *v.d.*, dorsal *v.v.*, ventral valve.

The digestive system

The alimentary canal is of the usual type for the articulates (Hancock, 1858; Joubin, 1892 ; Delage & Hérouard, 1897), and is without an anus. It will not be described in detail here, as it is hoped in a later paper to give a comparative account of the digestive system in brachiopods, but as publication is likely to be delayed by the pressure of other work it may be appropriate to make short reference to work already done.

The mouth, a median transverse opening at the depth of the food groove, leads into a narrow foregut, or oesophagus, which in *Pumilus antiquatus* is short (Fig. 6 C). In certain other articulates—*Terebratulina*, *Gryphus*, *Platidia*, *Macandrevia* and *Terebratella*—it is clearly divisible into a long anterior and a short posterior portion, separated by a valve-like elevation of the wall, of peculiar histological appearance. This may be the " léger

étranglement " which Joubin (1892) noted in *Magellania venosa* (Solander). A similar valve-like elevation was described by Yatsu (1902) as occurring in the larva and post larva of *Lingula unguis* (L.)—or as he called it, *L. anatina* Lamarck—and according to him marks the junction of ectoderm and endoderm. This junction was identified with difficulty in *Pumilus antiquatus* owing to the direction in which it was cut and the indifferent preservation.

The foregut has a sheath of connective tissue in which are circular and some longitudinal muscle fibres. The circular tend to be in bundles and are clearly striated. Striated fibres have also been distinguished in this position in *Tegulorhynchia nigricans*, *Macandrevia cranium* and *Terebratella inconspicua*, but not so far in species of the other genera mentioned above. It seems doubtful, however, that the oesophageal muscles are striated in some species and not in others, as all feed in the same manner. Inability to distinguish striations may be due to faulty fixation, staining, or perhaps to the state the muscles were in when fixed. In *Macandrevia cranium* it was observed that food entering the mouth passes down the foregut by ciliary action, but faecal matter is ejected by antiperistalsis. Antiperistalsis was seen by Richards (1952) to occur in *Neothyris lenticularis* (Deshayes).

The muscles of the stomach and intestine appear to be smooth.

The general structure and histology of the stomach and intestine of an articulate are known from the work of Joubin (1892) on preserved *Magellania* (= *Waldheimia*) *venosa* (Solander). He observed that " L'estomac renferme un épithélium très développé et à très grands cils vibratiles. Son contenu est formé de masses de mucosité disposées, sur des coupes en spirale, comme si les cils vibratiles, faisant toujours tourner les aliments dans le même sens, l'enroulaient peu à peu. Les aliments au centre de la spirale sont plus tassés qu'à la périphérie ; ils s'engagent dans l'intestin où ils perdent bientôt cette disposition particulière ". While the stomach contents do rotate in a clockwise direction viewed anteriorly, it was found from work on *Macandrevia cranium* that this is due to cilia in two separate regions. Over the greater part of the stomach wall the cilia beat longitudinally : on the dorsal and lateral walls currents pass backwards and then curve round ventrally toward the deep longitudinal groove of the intestine, with its long posteriorly beating cilia. In the mid-ventral line of the stomach a swift current runs anteriorly. The two regions in which clockwise rotation of the stomach contents is effected is first in the stomach just posterior to the entrance of the oesophagus. Here material, perhaps chiefly from the diverticula, is compacted into a bolus or string with mucoid substance, by the rotating action of the cilia. The second region is in the intestine, where the cilia, fairly short except for those in the longitudinal groove, beat obliquely transversely. A string of particles entangled in a viscid, colourless, transparent substance and rotated clockwise viewed anteriorly, projects into the stomach and may be considered a protostyle (see Morton, 1952). This protostyle has been seen stretching through the length of the stomach, when it then comes under the influence of the clockwise beating cilia of the anterior region : it is thus rotated at both ends.

The intestine of the articulates corresponds histologically and in the appearance and action of its cilia in life, with what Joubin (1886) called the

posterior funnel-shaped part of the stomach in the inarticulate, *Crania anomala*. But he would seem to have been somewhat undecided whether this region should be considered stomach or intestine for he described it under both sections : it would seem unlikely that he meant to imply that the junction between stomach and intestine occurred in the funnel. On p. 232 he stated that " La troisième partie (of the stomach) a la forme d'un entonnoir qui se continue par l'intestin ", while on p. 233 he said " L'intestin fait suite à l'estomac, commence par une portion en forme d'entonnoir, et se continue par un tube ayant le même diamètre dans toute son étendue ". He noted that the funnel shaped portion was separated from the rest of the stomach by " un rétrécissement ".

The intestine of brachiopods with its rotatory cilia may be compared with the style sac of Mollusca. In molluscs the style sac would seem to be a specialized tube which has become divided longitudinally from the intestine (Graham, 1934 ; Morton, 1952). By analogy with the style sac of molluscs the posterior part of the gut in the articulates may be considered to be intestine, as it has been formerly. Moreover, during development it arises as an outgrowth from the enteron (Percival, 1944).

In *Pumilus antiquatus* the digestive gland enters the anterior region of the stomach by a single duct on each side (Fig. 7 A), and in large individuals the ramifications of the diverticula extend in the coelomic cavity as far forward as the anterior border of the lophophore.

The gonads and the nephridia

The gonads consist of a ventral and dorsal pair of glands (Fig. 7). The posterior limit of the germinal bands is at about the level of the large, internal openings of the nephridia. The ventral pair extend into the paired mantle sinuses to about two thirds of the length of the pedicle valve. The dorsal pair are more or less confined to the coelomic cavity, anteriorly reaching almost to the posterior base of the lophophore, but laterally are continued into two short pockets one on each side of it, separated from the main visceral cavity by membranes which are continuations of the gastro-parietal bands (Fig. 7 A).

Only eight specimens have been sectioned, but from these it is evident that *P. antiquatus* is hermaphrodite. It would appear that the gonads develop early, and that the species is sexually mature at a small size.

In two specimens of 1·7 and 1·95 mm. shell length preserved on 30th July 1957 after travelling from New Zealand by boat, the dorsal glands were undeveloped. In the smaller of the two, the ventral glands contained a few ova up to $70 \times 100\,\mu$ and these were present as far anteriorly as the region of the oesophagus. In the larger individual, eggs of $70 \times 80\,\mu$ extended into the ventral mantle sinuses. In both animals small groups of what appeared to be spermatocytes were present in the germinal bands, so far as could be ascertained from material not in perfect condition when preserved.

A specimen of shell length 2·65 mm. preserved in formalin on 30th March 1941 had both ventral and dorsal glands containing large ova, and possibly small areas of spermatocytes, but fixation was poor.

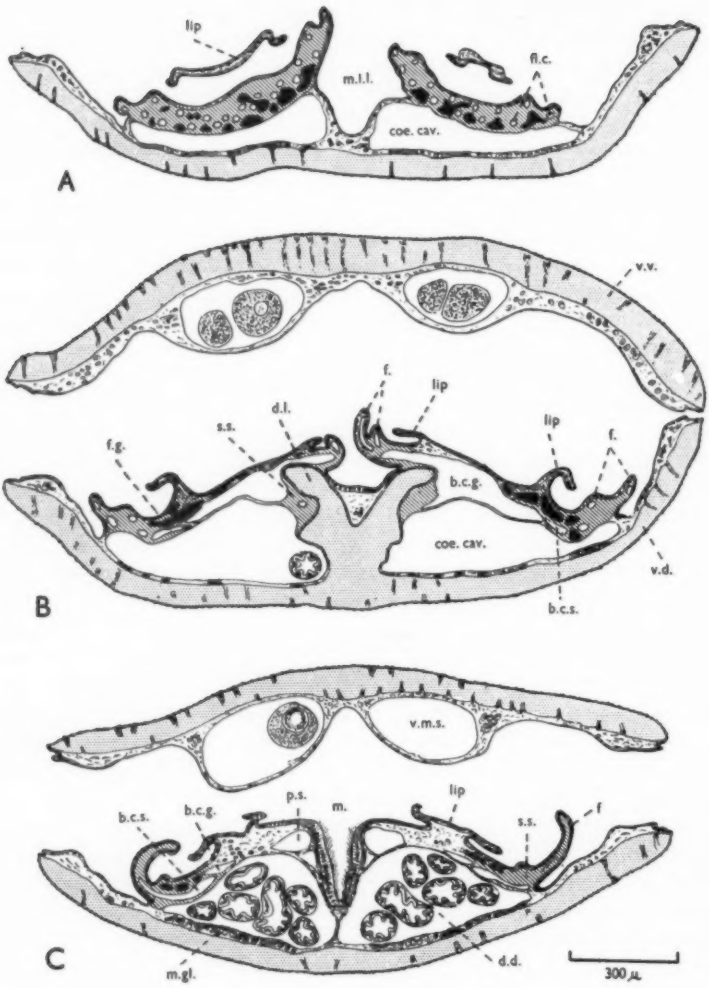


Fig. 6.—*Pumilus antiquatus*. Transverse sections of specimens of shell length 2·9 mm. (A & B) and 2·65 mm. (C).

A. Through the anterior region of the lophophore : ventral valve omitted.

B. Through the posterior end of the median invagination of the lophophore, where new filaments arise.

C. Through the mouth : disposition of the diverticula is normal.

b.c.g, great and *b.c.s.*, small brachial canals ; *coe. cav.*, coelomic cavity ; *d.d.*, digestive diverticula ; *d.l.*, divergent lamella ; *f.*, filament or filament base ; *fl.c.*, filamentar canal ; *f.g.*, food groove ; *lip*, lip of food groove ; *m.*, mouth ; *m.gl.*, mucous glands ; *m.i.l.*, median invagination of lophophore ; *p.s.*, perioesophageal sinus ; *s.s.*, supporting substance ; *v.d.*, dorsal and *v.v.*, ventral valve ; *v.m.s.*, ventral mantle sinus.

Black areas indicate spaces formerly occupied by spicules : cilia shown in the gut only : filaments cut in transverse and oblique section omitted.

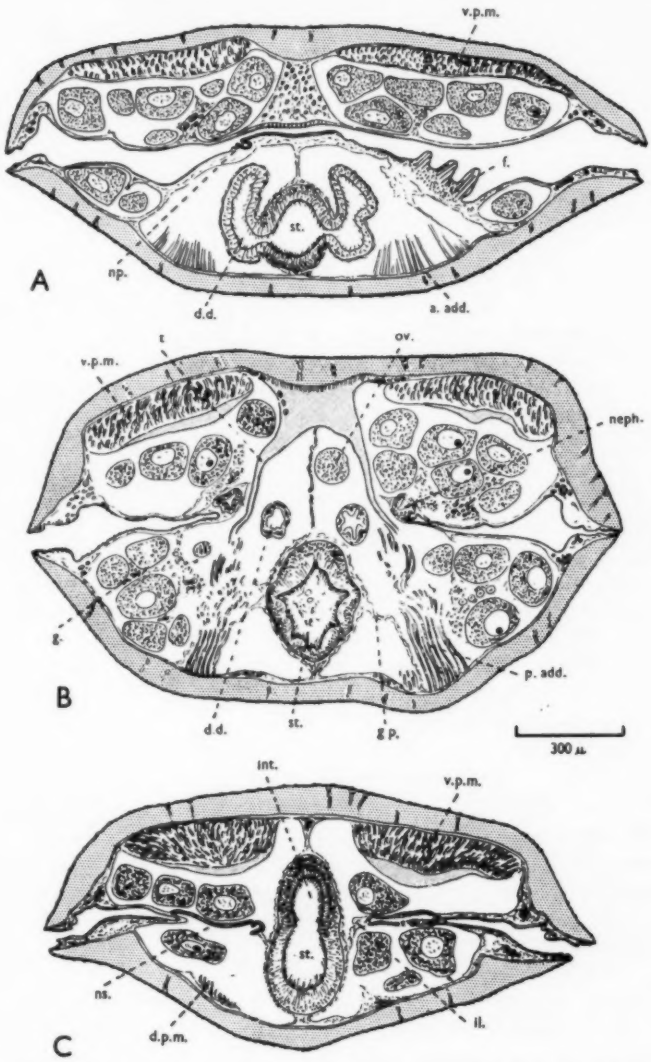


Fig. 7.—*Pumilus antiquatus*. Transverse sections of specimens of shell length 2·8 mm. (A & C) and 2·9 mm. (B).

A. Immediately posterior to the lophophore, but slightly oblique so that the bases of three filaments (*f*). are cut on the right.

B. Through the stomach and posterior adductor muscles (*p.add.*).

C. Through the nephrostomes (*ns.*) and junction of the stomach and intestine (int.).

a.add., anterior adductor muscle ; *d.d.*, digestive diverticulum and tubule ; *d.p.m.*, dorsal pedicle muscle ; *g.*, gonad ; *gp.*, gastro-parietal band ; *il.*, lateral ilio-parietal band ; *neph.*, nephridium ; *np.*, nephridiopore ; *ov.*, ovum ; *p.add.*, posterior adductor muscle ; *st.* stomach ; *t.*, tendon of adductor muscle ; *v.p.m.*, ventral pedicle muscle. Cilia indicated in the gut only.

Two *P. antiquatus* of shell length 2·8 mm. (Fig. 7 A, C) and 2·9 mm. (Figs. 6 B, 7 B) had the gonads fully developed, containing large ova, some $130 \times 150\,\mu$, with a few clusters of darkly staining cells, probably spermatocytes. These specimens were collected by Mr G. Owen in June and possibly the latter half of May, that is shortly after the breeding season of *Terebratella inconspicua* in the same locality, which Percival (1944) gives as early April to late May, with its greatest intensity during May. The ova of *Pumilus antiquatus* are larger than those of the brachiopods listed by Senn (1934, pp. 137–141). Percival (1944), however, records that eggs from the mantle cavity of *Terebratella inconspicua* are about $180\,\mu$ in diameter.

In an individual of shell length 3·2 mm. collected at about the same time as the two preceding ones the ova had been largely shed to the exterior, although some large ones still remained (Fig. 8). Male sex cells were well developed in the dorsal and ventral glands of one side of the body, tailed sperm being present. The male part of the gonads had evidently developed before all the ova had dropped into the visceral cavity, for its appearance suggested that it had fitted around the ova. In one ventral mantle sinus crowded with large ova, spermatids, or possibly spermatozoa, were present in the narrow spaces between the ova (Fig. 8 A).

Judging from this one specimen it seems possible that when ova drop into the coelomic cavity, they are not immediately passed to the exterior through the nephridia, but are stored there, where they become closely packed and compress the gut and digestive diverticula, even as far forward as the anterior region of the lophophore. It is interesting to compare the disposition of the diverticula in Fig. 8 with that in Fig. 6 C. For such compression to persist after shedding of the ova to the exterior, it would seem that they are stored in the cavity for some considerable time. There could be an alternative possibility that the eggs had fallen out during the process of sectioning and staining, but this seems unlikely as the animal was stained, cleared and examined before embedding and no ova could then be distinguished in the coelomic cavity beneath the lophophore. The specimen was received fixed in Bouin and so its history is unknown. It is possible that ova had been shed only a short time before fixation ; none, however, was present in the mantle cavity.

Storing of the ova in the coelomic cavity possibly allows of self fertilization.

The eighth specimen sectioned of shell length 3·5 mm. was in poor condition when preserved on 30th July 1957 and all that can be said of the gonads is that they contained large ova. The digestive diverticula and the gut were normal in position, indicating that ova had not been stored in the coelomic cavity, at any rate recently.

Senn (1934) described hermaphroditism in *Argyrotheca cuneata* (Risso) and *A. cordata* (Risso), and noting that the male and female parts of the gland reach their greatest development at the same time, concluded that there is simultaneous hermaphroditism. It has yet to be discovered whether this is so in *Pumilus antiquatus*, whether it is a protogynous hermaphrodite, or whether the gonads revert to the production of ova, and there is alternation in the production of sex cells. Senn (1934, p. 104) recorded specimens of *Argyrotheca*

cordata which had no ovaries, but the mantle sinuses filled with large testes, and concluded that the female part of the gland can sometimes be suppressed. It may be that development of the testes continues in *A. cordata*, as in *Pumilus*, after the shedding of the eggs.

The breeding, embryology, and larval development of *P. antiquatus* needs investigating by a worker in the district, able to procure material throughout the year and to fix it in good condition.*

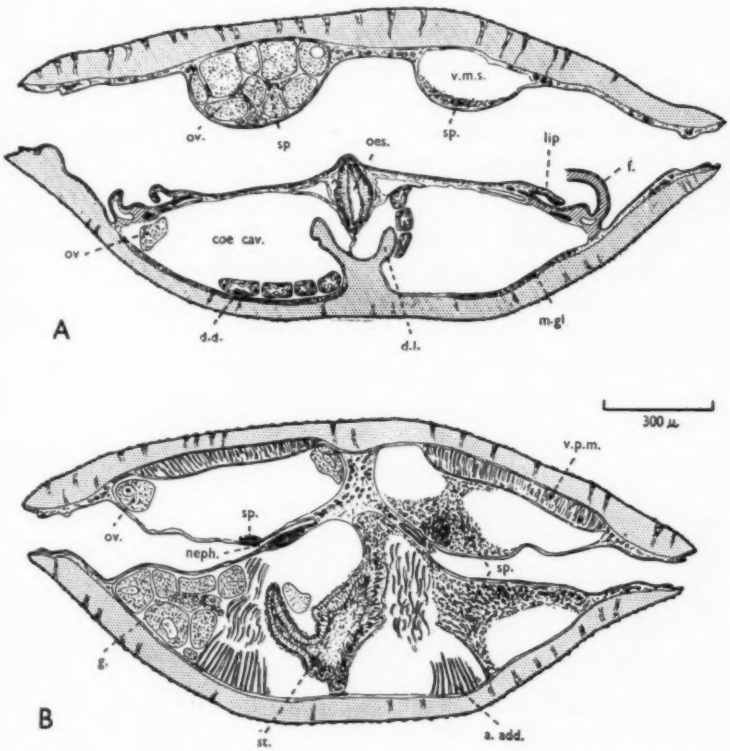


Fig. 8.—*Pumilus antiquatus*, transverse sections through an individual of shell length 3·2 mm. : many of the ova have apparently been shed.

A. Through the lophophore and the anterior region of the oesophagus (*oes.*). The digestive diverticula (*d.d.*) have been compressed and pushed to one side apparently by ova since shed.

B. Through the compressed stomach (*st.*) and the diverticulum of one side. The male gonad is well developed on the right : on the left some ova remain and male elements are backward in development.

a.add., anterior adductor muscle ; *coe. cav.*, coelomic cavity ; *d.l.*, divergent lamella ; *f.*, filament ; *g.*, gonad ; *lip.*, lip of food groove ; *m.gl.*, mucous glands ; *neph.*, nephridium; *ov.*, ovum ; *sp.*, male germ cells ; *v.m.s.*, ventral mantle sinus ; *v.p.m.*, ventral pedicle muscle.

Black areas indicate spaces formerly occupied by spicules : cilia indicated in the gut only.

* This work is now being done by Professor E. Percival.

The nephridia open at both ends and are therefore termed metanephridia, but may be nephromixia (Goodrich, 1945, pp. 117, 349). The single pair open internally by wide nephrostomes (*ns.* Fig. 7 C), which face dorsally, as in *Argyrotheca* (Shipley, 1883) and probably in all brachiopods. This opening was more convoluted in a specimen from which ova had been shed, than in those which appeared as yet to have shed none. The small external openings lie just behind the posterior border of the lophophore. That of one side (*np.*) is shown in the slightly oblique section illustrated in Fig. 7 A.

THE LOPHOPHORE

The structure of the adult lophophore

The adult lophophore is schizolophous, of the broad based terebratellacean type set low on the dorsal mantle (Figs. 6, 9, 10). There seems no doubt that this is so, for not only is *P. antiquatus* sexually mature with the lophophore in

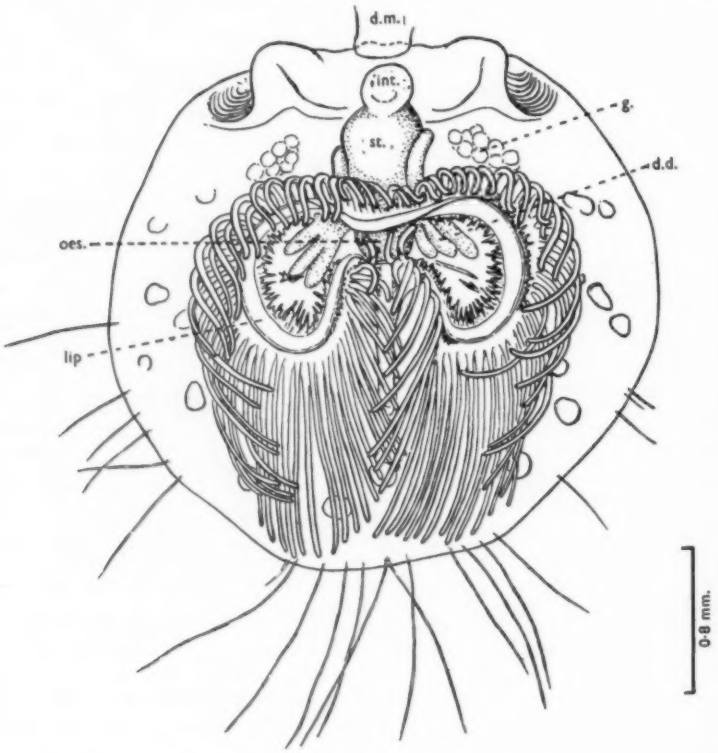


Fig. 9.—*Pumilus antiquatus* of shell length 3·8 mm. Brachial valve with lophophore, drawn living: many of the mantle setae have been shed. *d.d.*, digestive diverticula; *d.m.*, tendon of diductor muscles; *g.*, gonad; *int.*, intestine; *lip*, lip of food groove; *oes.*, oesophagus; *st.*, stomach; The septum and divergent lamellae are indicated; they were visible after fixing, staining and clearing in cedar wood oil.

this stage, but the growing region is not as crowded with young and budding filaments as in one in which the schizolophous condition is a growth stage.

The base of the lophophore is supported by spicules, which increase in number, size and complexity with age (Figs. 9, 11) : they are absent over the position of the oesophagus. The posterior end of the median invagination is supported by the divergent lamellae, which posteriorly approach the anterior face of the oesophagus. The lamellae raise the posterior and median part of the lophophore above the valve floor (Fig. 6 B), while anteriorly it is raised by the inflated coelomic cavity (Fig. 6 A). The floor of each side lobe thus slopes toward the mantle margins.

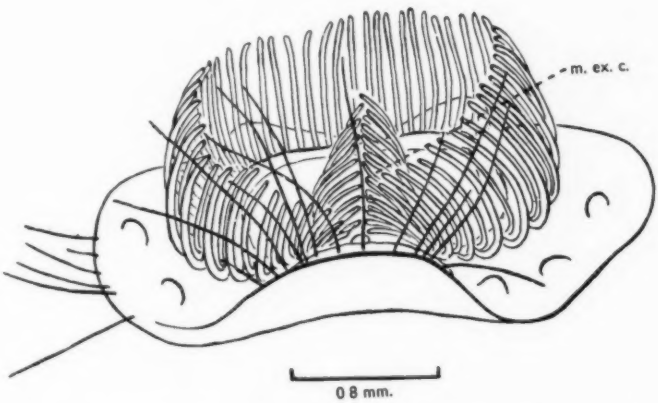


Fig. 10.—*Pumilus antiquatus*. Anterior view of brachial valve with lophophore, drawn living, but not fully expanded : same specimens as in Fig. 9. *m.ex.c.*, median excurrent channel.

The two series of alternating filaments characteristic of the great majority of recent brachiopods were described by Blochmann (1892, 1900) and Richards (1952) as inner and outer, the inner being the nearer to the brachial or food groove ; by Chuang (1956) they were termed adlabial and ablabial and by Orton (1914) ventral and dorsal. This double alternating series occurs in *P. antiquatus*—the inner with a ridged and the outer with a grooved frontal surface—except for some twenty filaments behind the mouth which are in a single series and are of the ridged type. Spicules are absent from the filaments.

The small or efferent canals (*b.c.s.* Fig. 6, p. 568) arise laterally from a well-marked perioesophageal sinus (*p.s.* Fig. 6 C) and pass around the lophophore at the bases of the filaments, to which are given off branches. Brachial canals (*b.c.g.* Fig. 6 B, C), probably representing the great or afferent brachial canals of more highly developed lophophores, are present. They end near the oesophagus, but not in a conspicuous sac on each side as in plectolophous lophophores. The coelomic cavity, divided into right and left halves, underlies the lophophore to its anterior extremity (*coe. cav.* Fig. 6).

Muscle fibres in the walls of the filamentar canals are most strongly developed in a frontal group (*f.m.* Fig. 13), and most, if not all, are striated :

a few small fibres to the outer sides of the group may possibly be smooth. A slight development of muscle fibres is present abfrontally (*abf.m.*), and these appear to be smooth, for after a careful search striations could not be found. Contraction of the abfrontal fibres would pull the filaments gently outwards into the expanded feeding position of the lophophore. The striated fibres would be responsible for the quick, flicking movements observed in a feeding animal, and for rapid incurving and coiling of the filaments preparatory to the closing of the valves. Filaments remain strongly coiled for long periods and this suggests that smooth fibres are present among the frontal group of striated fibres. Striated fibres are also present in the walls of the filamentar canals of the following articulate brachiopods : *Tegulorhynchia nigricans* (Sowerby), *Terebratulina retusa* (L.), *Argyrotheca cordata* (Risso), *Megathyris detruncata* (Gmelin), *Platidia davidsoni* (Deslongchamps), *Megerlia truncata* (L.), *Macandrevia cranium* (Müller) and *Terebratella inconspicua* (Sowerby), (unpublished work). Blochmann (1892, p. 42 ; fig. 76 f, g) described and figured striated fibres within the filaments of the inarticulate *Crania anomala* (Müller), while Chuang (1956, p. 175) stated that the filament muscle are smooth in *Lingula unguis* (L.).

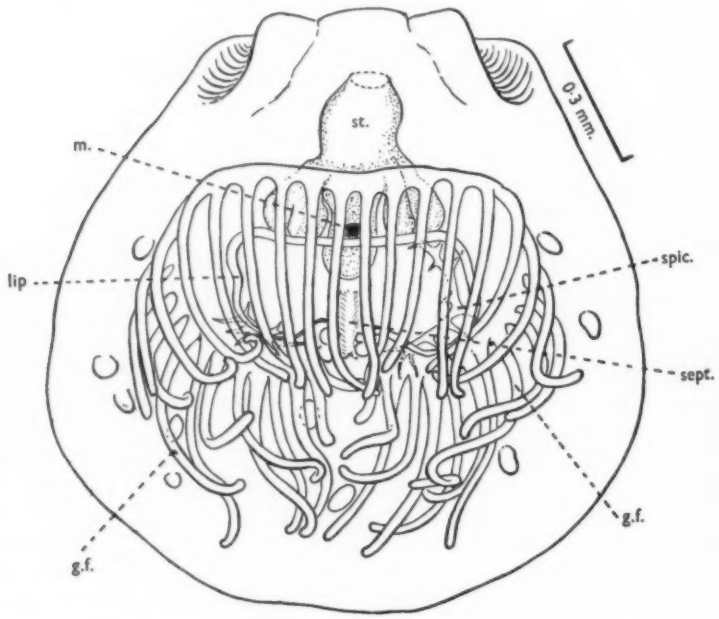


Fig. 11.—*Pumilus antiquatus* (shell length 1·8 mm.). Brachial valve with early schizolophous lophophore, drawn living but not fully expanded. The lip of the food groove (*lip*) is large and is almost erect. *g.f.*, first outer grooved filament on each side ; *m.*, mouth ; *sept.*, septum ; *spic.*, spicule ; *st.*, stomach. Mantle setae omitted.

Growth stages of the lophophore

The lophophore is trocholophous at a shell length of 1·0 mm. The only specimen of this size—since unfortunately lost—had been in formalin since 1941 and had become decalcified, but the presence of a median tubercle made its identification possible. At a shell length of 1·27 mm (Fig. 4 A, B, p. 563) an exceedingly low median ridge in the brachial valve represented the septum : divergent lamellae were lacking. Continuing the line of the median elevation were two tubercles, and in addition a submarginal tubercle was present on each side. Most of the tissue had disappeared ; it is probable, however, that the lophophore is still trocholophous at this size.

The lophophore was early schizolophous in two individuals of shell length 1·64 and 1·8 mm. (Fig. 11) : a few spicules supported its base. The brachial valve of another specimen of 1·8 mm. shell length is shown in three different aspects in Fig. 3 A–C (p. 562). Median and submarginal tubercles were large. The septum was higher than at a length of 1·27 mm., its ventral surface irregularly tuberculated anteriorly and showing slight indication of the growth of divergent lamellae.

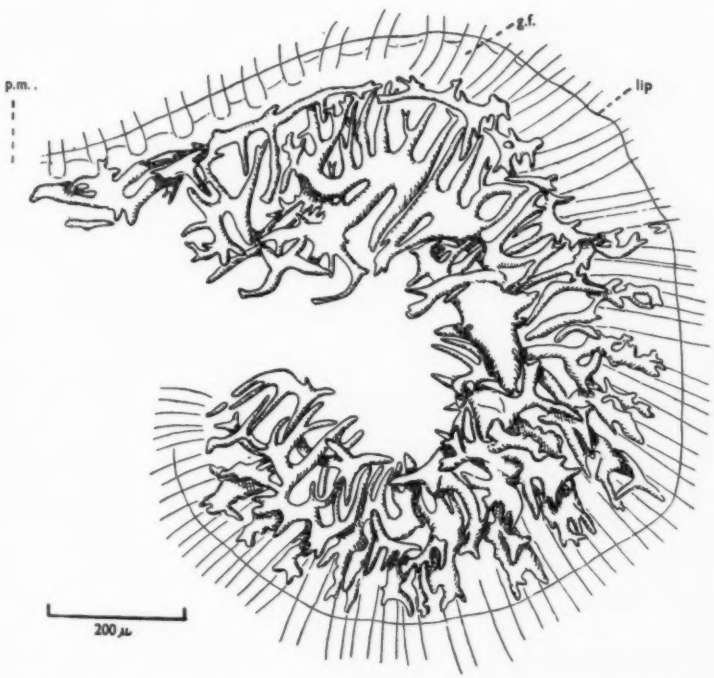


Fig. 12.—*Pumilus antiquatus*. Spicules of one half of an adult lophophore removed from the shell and viewed from the ventral side. All tissue gone, but cartilaginous supporting substance present.

g.f., first outer, grooved filament ; *lip.*, edge of lip of food groove ; *p.m.*, posterior median region of lophophore.

At a shell length of 2·2 mm. the lophophore was schizolophous ; the two sides of the median invagination supported by the lamellae.

With increased size the lamellae instead of supporting the sides of the median invagination support its posterior blind end, for example, at a shell length of 3·8 mm. (Figs. 9, 10). The spicules had increased in size and complexity and a few isolated ones were present in the brachial membrane or floor of the lateral lobes. In the largest individual seen of shell length 4·7 mm. the lophophore had not advanced beyond the schizolophous stage (Fig. 14), and there seems no reason to doubt that this is the final stage attained : spicules had still further increased in size and complexity. Those of one half of an adult lophophore are shown in Fig. 12 : the size of the specimen from which this was taken is unknown.

THE CILIARY FEEDING MECHANISM

The ciliation of the lophophore and of the mantle

The frontal cilia of the filaments (*f.c.* Fig. 13) are long and are capable of reversing their beat, as in thirteen other genera of brachiopods examined (Atkins, 1956 and unpublished work).

The lateral cilia (*l.c.* Fig. 13) beat from the frontal to the abfrontal surface with a characteristic metchronal wave, designated dexioplectic by Knight-Jones (1954, p. 515). These are the cilia which produce the water currents.

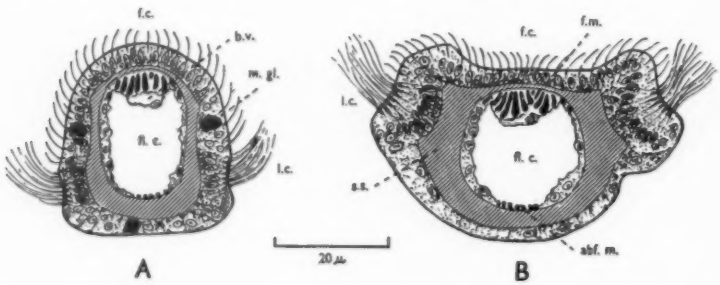


Fig. 13.—*Pumilus antiquatus*. Transverse sections, somewhat diagrammatic, of : A. Inner, ridged filament : B. Outer, grooved filament.

abf.m., abfrontal muscle fibres ; *b.v.*, ' blood ' vessel ; *f.c.*, frontal cilia ; *fl.c.*, filamentar canal ; *f.m.*, frontal group of muscle fibres shown black ; *l.c.*, lateral cilia ; *m.gl.*, mucous gland ; *s.s.*, supporting substance.

The frontal cilia are not shown at their full length as they beat along the length of the filament.

Abfrontal cilia appear to be absent or few : no current could be demonstrated along the abfrontal surface of the filaments.

The floor, or brachial membrane, of the lateral lobes of the lophophore is ciliated ; particles pass on to the outer surface of the lip of the food groove and either into the groove or on to the frontal surfaces of the filaments according as to whether the lip is raised or fitting closely over the groove.

It appears to be characteristic of brachiopods that wherever ciliated epithelium occurs there is only one cilium or flagellum to a cell. Certain references to this occur in the literature. It was noted for the ciliated cells of the lophophore and of the body wall of *Crania anomala* by Blochmann (1892), for the gut epithelium of *Magellania* (=*Waldheimia*) *venosa* by Joubin (1892), for the epithelium of the stomach of the larva of *Pelagodiscus atlanticus* by Ashworth (1915) and for the lophophore epithelium of *Terebratulina retusa* (=*caput serpentis*) by Tuzet & Sanchez (1954).

From the few living individuals available it is only possible to state that the mantle is ciliated—as indicated by the wagging to and fro of particles adhering to the tips of cilia—although no mantle currents could be demonstrated. The demonstration of mantle currents in small species with large lophophores, including *Argyrotheca* and *Megathyris* in good condition, is frequently difficult.

The ciliary currents

Of the living specimens examined few were in a fair or passable state, and only one or two in a good state. Under unfavourable conditions the filaments are unfortunately the first structures to suffer deterioration and the epithelium quickly disintegrates. However, it was possible to make out the direction of the water and food currents.

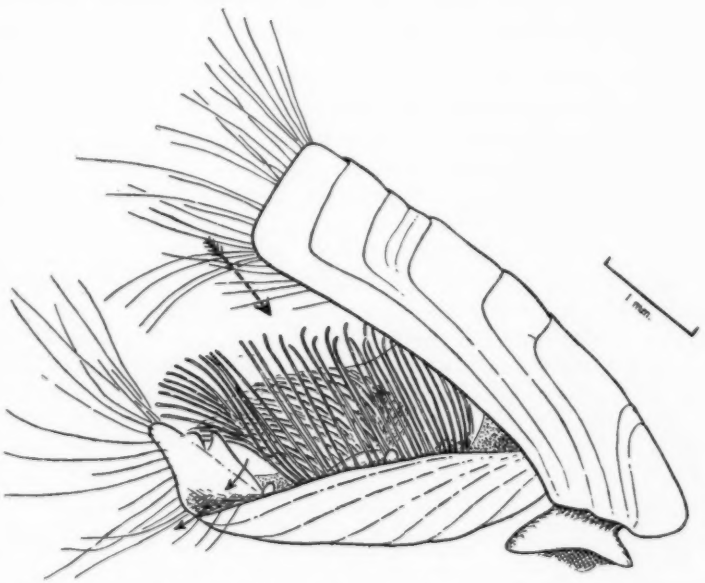


Fig. 14.—*Pumilus antiquatus* (Syntype A : shell length 4·7 mm.). Lateral view of animal drawn preserved after narcotising ; the shell is possibly gaping somewhat more than in life. A barbed arrow indicates the main inhalant current before it has divided into right and left streams. Two small arrows indicate the probable direction of the current leaving the shell from the median excurrent channel.

As with schizolophous lophophores generally, whether adult or adolescent, paired inhalant currents set into the side lobes and the exhalant current escapes between the filaments, leaving the shell mainly laterally. A narrow median excurrent channel walled by the filaments of the median invagination (*m. ex. c.* Fig. 10) is possibly the path for the conveyance of waste matter from the mouth. In adults the filaments at the anterior end of the channel touch on the well marked sulcus in the brachial valve (Fig. 14) and it is probable from this disposition that the current will tend to leave the shell antero-laterally instead of anteriorly.

On the frontal surfaces of the filaments particles pass either toward the base or toward the tip, according to the size and quantity of particles provided. Those travelling in the former direction arrive in the food groove along which they pass toward the mouth. Those travelling toward the tip are finally rejected from the shell. In the few specimens watched there was a greater tendency for particles to pass to the tip rather than to the base on the inner, ridged filaments and for the opposite to occur on the outer, grooved filaments. This has been observed also in other species. A probable explanation is that as the ridged filaments are in advance of the grooved they receive on their frontal surfaces much of the material in the inhalant current. This, if coarse or in quantity, stimulates the frontal cilia to beat toward the tip, and the unwanted food is rejected from the shell. The fine particles remaining in the current pass between the inner series of filaments and impinge on the frontal surfaces of the outer, grooved filaments, down which they travel to the food groove.

DISCUSSION AND AFFINITIES

It would not seem possible to place this new species in any known genus, and a new one, *Pumilus*, has been created.

Other known genera with schizolophous lophophore in the adult are *Amphithyris* and *Argyrotheca*.

Amphithyris buckmani Thomson, from Cook Strait, New Zealand has a shell length and breadth of 5 mm. Thomson in his original description (1918, p. 22) described the filaments as being in a single row : in his later work (1927, pp. 215–216) he did not repeat this statement and it is therefore uncertain whether or no *Amphithyris* has indeed only one row of filaments. His original description was based on a single specimen which he recorded had been dead and rotting for a fortnight before it came into his hands (1918). Later he obtained young specimens with trocholophous lophophore up to a shell length of 1·5 mm. (1927, p. 217). In any case *Amphithyris* differs widely from *Pumilus* in shell shape and beak characters, and in the brachial support, which in the former is a fairly high median septum. Both have the lophophore supported by spicules.

Pumilus differs from *Argyrotheca* in beak characters, in the type of brachial support, in strong spiculation of the lophophore, and above all in the arrangement of the filaments. In *Pumilus* the filaments are in a double alternating series, except for some twenty behind the mouth, while in *Argyrotheca cordata* (Risso) and *A. cuneata* (Risso) and also in *Megathyris detruncata* (Gmelin)

filaments are in a single row and all of the same kind. This was remarked by Dall (1871, p. 22) to be so in *Argyrotheca* (=*Cistella*) *lutea* (Dall) and other species of the genus. Both Shipley (1883) and Schulgin (1885) figure only a single row of filaments in *Argyrotheca*. The arrangement of filaments in a single series is possibly primitive, for, with the exception of *Lingula* (one specimen only seen), all those species, including *Crania anomala*, examined, which had a double series, yet had a certain number in single series behind the mouth. These latter are the earliest formed filaments, present in the trocholophous stage and retained in the adult.

Although the arrangement of the muscles in *Pumilus antiquatus* is similar to that in *Argyrotheca* (Shipley, 1883) the structure of the adductors is apparently different. The posterior adductors of the new species are composed of clearly striated fibres. Shipley stated that these muscles were unstriated in *Argyrotheca* : I have been unable to detect striations in the posterior adductors of either *Argyrotheca* or *Megathyris*, but as striations when known to be present cannot always be demonstrated, I feel hesitant of stating that they are absent. The lack of striation in the posterior adductors of these two genera is curious, as striated fibres are not entirely absent, being present in the filaments.

The brachial apparatus of *Pumilus* may be compared with that of the young of *Kraussina rubra* (Pallas) as described and figured by Elliott (1949). The divergent lamellae, however, differ from those of the young of that species in being lower and generally triangular in shape, although they are occasionally rectangular as in *Kraussina rubra*.

Among the kraussinids the only species previously known with smooth shell was *Kraussina atkinsoni* (Tenison-Woods) from Long Bay, South Tasmania in 10 fathoms of water (Davidson, 1887, p. 127). It, like *Pumilus antiquatus*, is a small species of little more than 6 mm. shell length, with pronounced and early sulcation (Thomson, 1927, p. 224). In lateral profile the two are not unlike, but in *K. atkinsoni* the beak is incurved. The latter species has a smaller foramen, a more advanced brachial skeleton and apparently lacks tubercles on the inner surface of the valves (Davidson, 1887, pl. 21, Fig. 6) : it is a species of which little is known. Tuberculation is not uncommon in kraussinids ; it occurs in the adults of *Megerlina lamarckiana* (Davidson), *M. davidsoni* (Vélain) (Davidson, 1887, pp. 124, 126), *Megerlia truncata* (L.) and *Pantellaria echinata* (Fischer & Œhlert) (Fischer & Œhlert, 1891, pl. vii).

The ridges running inwards from the inner socket ridges in *Pumilus antiquatus* and marking the anterior edges of the dorsal pedicle muscle scars are to be found also in *Megerlina lamarckiana*, a shallow water species from Australia (Thomson, 1927, p. 225). Thomson noted that the cardinalia had been inaccurately depicted by Davidson (1887, pl. 21, Fig. 11), according to whom the hinge plate is similar to that of *Kraussina rubra*, with two eye-shaped rudimentary scars due to the dorsal pedicle muscles. Slight delimiting ridges are also present in *K. atkinsoni* (Mr. G. F. Elliott *in lit.*).

In those kraussinids in which the lophophore has been described however briefly—*Kraussina rubra*, *Megerlina lamarckiana* and *Megerlia truncata*

(Davidson, 1887)—it is plectolophous with a short spiral arm : it has unfortunately not been described in *Kraussina atkinsoni*.

It is proposed to place *Pumilus* in the Kraussinidae (Allan, 1940) for the following reasons :—(1) the brachial skeleton resembles that of immature *Kraussina rubra* ; (2) the presence of spicules in the lophophore (present also in *Megerlina davidsoni* and in *Megerlia truncata*) ; (3) similar arrangement of muscles to that in *Megerlia*, with the posterior adductors striated. The muscular system of *Kraussina* has not yet been described in detail.

ACKNOWLEDGMENTS

I am particularly indebted to Professor E. Percival for the care he has taken in collecting and packing live New Zealand brachiopods and the enthusiasm with which he persisted in his attempts to get them to me in good condition. My thanks are due also to Mr G. Owen for preserved material and to Mr A. C. G. Best for the photographs in the Plate. Mr G. F. Elliott most kindly read the manuscript and commented on the part dealing with the affinities of the species.

A grant from the Browne Fund of the Royal Society and a London University Table enabled me to continue work on brachiopods begun while holding a Leverhulme Research Fellowship 1953–55. The work on *Pumilus* itself was done with the aid of the former grant : that on *Macandrevia*, *Terebratulina* and *Crania*, to which reference is made, was carried out during the Leverhulme fellowship.

SUMMARY

A new species and genus, *Pumilus antiquatus*, of kraussinid brachiopod from shallow water, Lyttelton, New Zealand, is described and figured. It is characterized by the possession of a schizolophous lophophore in the adult, supported by both divergent lamellae and spicules : the shell is smooth, less than 5 mm. long and strongly sulcate. The gonad is hermaphrodite.

Notes are given on the ciliary feeding mechanism.

The affinities of *P. antiquatus* are briefly discussed : it is placed in the Kraussinidae.

REFERENCES

Allan, R. S. (1940). A revision of the classification of the Terebratelloid Brachiopoda. *Rec. Canterbury (N.Z.) Mus.* **4**, 267.

Ashworth, J. H. (1915). On larvae of *Lingula* and *Pelagodiscus* (*Discinisca*). *Trans. roy. Soc. Edinb.* **51**, 45.

Atkins, D. (1956). Ciliary feeding mechanisms of brachiopods. *Nature, Lond.* **177**, 706.

Blochmann, F. (1892). *Untersuchungen ueber den Bau der Brachiopoden.* Theil I. Jena : Gustav Fischer.

Blochmann, F. (1900). *Untersuchungen ueber den Bau der Brachiopoden.* Theil II. Jena : Gustav Fischer.

Chuang, S. H. (1956). The ciliary feeding mechanisms of *Lingula unguis* (L.) (Brachiopoda) *Proc. zool. Soc. Lond.* **127**, 167.

Dall, W. H. (1871). Report on the Brachiopoda obtained by the United States coast survey expedition. *Bull. Mus. comp. Zool. Harv.* **3**, 1.

A 1

A 2

B 1

B 2

Pumilus antiquatus gen. and sp. n.

DAVIDSON, T. (1887). A monograph of recent Brachiopoda.—Part II. *Trans. Linn. Soc. Lond.* (Zool) (2) **4,** 75.

DELAGE, Y & HÉROUARD, E. (1897). *Traité de Zoologie Concrète.* 5. *Les Vermidiens.* Paris : C. R. Schleicher Frères.

ELLIOTT, G. F. (1949). The brachial development of *Kraussina* (Brachiopoda). *Ann. Mag. nat. Hist.* (12) **2,** 538.

FISCHER, P. & ŒHLERT, D. P. (1891). Brachiopodes. *Expéd. sci.* '*Travailleur*' *et du* '*Talisman*'.

GOODRICH, E. S. (1945). The study of nephridia and genital ducts since 1895. *Quart. J. micr. Sci.* (n.s.) **86,** 113.

GRAHAM, A. (1934). Structure and relationships of lamellibranchs possessing a cruciform muscle. *Proc. roy. Soc. Edinb.* **54,** 158.

HANCOCK, A. (1858). On the organization of the Brachiopoda. *Phil. Trans.* **148,** 791.

JOUBIN, L. (1886). Recherches sur l'anatomie des brachiopodes inarticulés. *Arch. Zool. exp. gén.* (2) **4,** 161.

JOUBIN, L. (1892). Recherches sur l'anatomie de *Waldheimia venosa* (Sol.). *Mém. Soc. zool. France* **5,** 554.

KNIGHT-JONES, E. W. (1954). Relations between metachronism and the direction of ciliary beat in Metazoa. *Quart. J. micr. Sci.* (n.s.) **95,** 503.

MORTON, J. E. (1952). The role of the crystalline style. *Proc. malac. Soc. Lond.* **29,** 85.

ORTON, J. H. (1914). On ciliary mechanisms in brachiopods, etc. *J. Mar. biol. Ass. U.K.* (n.s.) **10,** 283.

PERCIVAL, E. (1944). A contribution to the life-history of the brachiopod, *Terebratella inconspicua* (Sowerby). *Trans. roy. Soc. N.Z.* **74,** 1.

PERCIVAL, E. (1953). Orientation of Telotrematous Brachiopoda. *Nature,* Lond. **171,** 436.

RICHARDS, J. R. (1952). The ciliary feeding mechanism of *Neothyris lenticularis* (Deshayes). *J. Morph.* **90,** 65.

SCHULGIN, M. A. (1885). *Argiope Kowalevskii. Z. wiss. Zool.* **41,** 116.

SENN, E. (1934). Die Geschlechtsverhältnisse der Brachiopoden, im besonderen die Spermato- und Oogenese der Gattung *Lingula. Acta zool., Stockh.* **15,** 1.

SHIPLEY, A. E. (1883). On the structure and development of *Argiope. Mitt. zool. Sta. Neapel,* **4,** 494.

THOMSON, J. A. (1918). Brachiopoda. *Sci. Rep. Aust. antarct. Exped.* **1911–14,** (C) **4,** pt. 3.

THOMSON, J. A. (1927). *Brachiopod morphology and genera* (*Recent and Tertiary*). Wellington : New Zealand Board of Sci. and Art : Manual 7.

TUZET, O. & SANCHEZ, S. (1954). Sur la présence d'un appareil parabasal dans les cellules flagellées des bras du brachiopode, *Terebratulina caput serpentis L. C. R. acad. Sci., Paris,* **238,** 1839.

YATSU, N. (1902). On the development of *Lingula anatina. J. Coll. Sci. Tokyo* **17,** art. 4.

EXPLANATION OF THE PLATE

Figs. A 1 & A 2.—Syntype A ; shell length 4·7 mm. and width 3·4 mm. A 1, brachial view ; the pedicle is present : A 2, pedicle view.

Fig. B 1 & B 2.—Syntype B ; shell length 4·3 mm. and width 3·3 mm. B 1, brachial view : B 2, pedicle veiw.

All photographed while in water. Mantle setae omitted.

ON THE DIET AND FEEDING HABITS OF THE EDIBLE FROG (*RANA ESCULENTA* LINNAEUS)

BY

MICHAEL J. TYLER

175 *Waldegrave Road, Teddington, Mddx.*

[Accepted 11th March 1958]

(With 5 figures in the text)

CONTENTS

	Page
Introduction	583
Methods	585
Observations	586
Discussion	593
Acknowledgments	594
Summary	594
References	594

INTRODUCTION

During the past fifty years the stomach contents of many species of the Anura have been examined to ascertain their diets, and the striking dissimilarities in the prey recovered has led many authors to discuss at great length the evidence for and against the problem as to whether frogs are selective in their feeding habits.

The stomach contents of several thousands of frogs and toads of no less than sixty-three species, collected by the expeditions of the American Museum of Natural History to Nicaragua and the Belgian Congo, were examined by Noble (1918 & 1924), whilst Cott (1932) has examined the prey from several species of tree frogs captured in Portuguese East Africa and the Lower Zambesi Valley. Of the species of Anura indigenous to the British Isles, the latter author (1957) has examined prey from *Bufo bufo vulgaris* and *Rana temporaria* whilst that of *R. ridibunda* has been examined by Smith (1953).

Other important contributions on *Rana* have been made by Needham (1905) on *R. catesbiana*; Drake (1914) on *R. pipiens*, and Liu & Chen (1932) on *R. limnocharis* and *R. nigromaculata*.

Although mention has been made by several authors to items of food recovered from the stomachs of the Edible Frog (*R. esculenta*), the present paper describes the first comprehensive examination of the prey of this species.

Angel (1946) states that *R. esculenta* is carnivorous and lists the following food items: worms, larvae, molluscs, insects, other young batrachians and the eggs and young of fish. Rather a conflicting view is expressed by Smith (1951, p. 145) who states. "... The main diet of the Edible Frog appears to be insects of various kinds, chiefly beetles, which it catches on land." Boulenger (1897) states that large specimens will occasionally capture snakes and small mammals and birds.

The Edible Frog has a very limited distribution in Great Britain and is now restricted to a few localities in south-east England (Smith, 1952 and 1954). It would therefore be impossible to examine the stomach contents of a large number of frogs in this country without seriously depleting several colonies.

Whilst on holiday in France in 1953 I observed several large colonies of Edible Frogs at Senonches: a small village in the region of Eure-et-Loir situated 100 miles west of Paris. I returned to Senonches in August 1957 with Mr P. J. Ratcliff and, by camping near one of the colonies, was able to conduct a detailed survey at all hours of day and night.

The majority of the frogs examined were captured in a lake on the southern outskirts of Senonches, known as L'Etang de Badouleau. This lake had a surface area of approximately 100,000 sq. ft., and was bounded by dense pine forest, heath and arable land. It was congested with pond weeds and, in two clearly defined regions, tall rushes dominated the vegetation. The surface of the water was covered with insect-pollinated flowers.

The available insect prey is dependent upon the type of vegetation within any particular habitat. Since L'Etang de Badouleau was bounded by several different types of vegetation, it was expected to provide a greater variety of available insect prey than could be normally found at one locality.

During a drought in the summer of 1953, when the lake dried up, the frogs migrated to irrigation ditches in the nearby arable land but, according to local reports, returned in the spring of 1954. The summer rainfall (Table 1) of 1954–1957, together with the more skilful use of a small sluice gate, enabled the water level to be kept nearly constant. The approximate water depth is shown in Fig. 1.

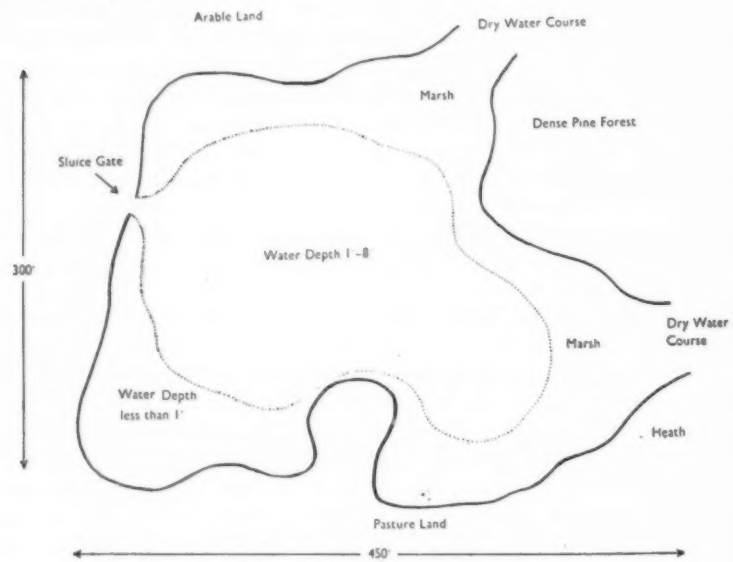


Fig. 1.—Sketch map of L'Etang de Badouleau.

TABLE 1

Monthly rainfall for Chartres (Eure-et-Loir) in millimetres

	1953	1954	1955	1956	1957	Normal (Mean 1901–30)
July	59	24	113	46	97	51
August	14	51	13	61	25	44
September	53	66	38	40	70	55

Monthly rainfall figures for Senonches for the period 1953–57 are not available and those for Chartres, a city 25 miles due east, are shown instead. The comparable monthly mean figures for Senonches for the period 1901–30 are: July, 58 mm.; August, 44 mm.; September, 50 mm. [Taken from data in possession of The Director General of the Meteorological Office, London.]

METHODS

(*a*) *Methods of capture employed*

Smith (1951) has stated that the method of capture employed upon the Continent is to fish with rod and line, using a small strip of brightly coloured material as bait.

The rod of thin bamboo cane is so held that, when it is made to quiver, the bait bounces upon the surface of the water. The criterion for success is several hours of continuous sunshine and, in 1953 when such conditions prevailed, I caught as many as twenty-five mature frogs in an hour by this method. During August 1957 the temperature was well below the normal for Eure-et-Loir at that time of the year, and my attempts at angling during the short periods of sunshine were unsuccessful.

It was stated by the villagers that the phase of the moon affected the activities of the frogs, but I did not capture the frogs over a long enough period to draw any conclusions as to the validity of this statement.

The power of sight of the Edible Frog is not to be under-estimated for, during the daytime, a group would swim en masse for cover when I approached to within 120 ft. of them.

At night the frogs come to the surface of the water and it was noticed that, if a powerful torch was shone upon the surface, those within the beam and facing the source of light did not move, and appeared to be incapable of movement. Those which were so orientated that they were not directly facing the source of light quickly swam away and submerged. Holding a torch well in front of my body I was able to approach to within one foot of the frog selected for capture. It was then possible to place a net in the water behind the frog and knock the creature into the net using the free fingers of the hand engaged in holding the torch.

Frogs which had recently metamorphosed were captured by hand at the water's edge and, together with more mature frogs, were also collected from heaps of rotting vegetation dragged by hand from shallow regions of the lake.

(*b*) *Examination and preservation of specimens*

Promptly after capture all specimens of *R. esculenta* were measured, examined and then killed by destroying the brain with a dissecting needle. (The only drawback to the use of this method was that, upon occasions, the

needle used penetrated the roof of the buccal cavity and blood trickled down the oesophagus into the stomach and made the later identification of the contents difficult.) The stomach was then removed and, prior to preservation in a 5 per cent formalin solution, was incised to permit the preservative to enter rapidly and thus prevent any further digestion of the contents.

Whenever possible, the contents of the ileum were examined; the bladder and lungs were opened and a search made for the presence of any parasites.

Abnormalities in the structure or condition of organs associated with the alimentary canal were recorded.

OBSERVATIONS

1. *Remarks upon relationship between the diet and the size of the frog*

The measurements of sixty-three frogs (distance between external nares and vent) are analysed in the histogram shown in Fig. 2 and, from the numbers

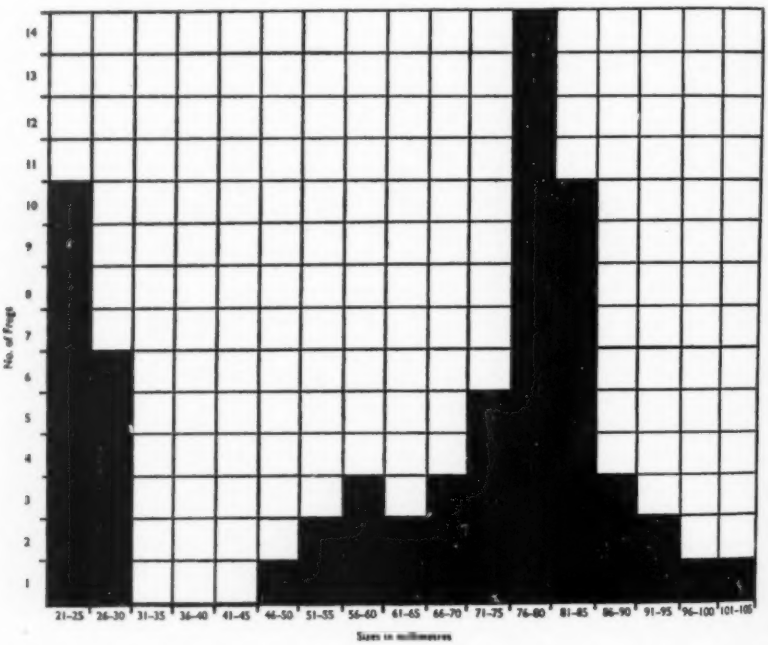


Fig. 2.—Histogram of the sizes of frogs captured (distance between external nares and vent measured in millimetres).

of frogs within certain size categories and their absence in others, I conclude that the ages of the specimens could be approximately estimated as follows:

First year : 22– 29 mm.
Second year: 45– 73 mm.
Third year : 76– 93 mm.
Fourth year: 98–104 mm.

The slight variation in the sizes of the first-year frogs which had just completed metamorphosis was probably due to differences in the dates of laying of the spawn from which they had developed.

The difference in size between the first- and second-year frogs is clearly defined, but there is not a similar gap in the histogram to separate the second year from the third year. In view of the possibility that overlapping could therefore occur, and also that the majority of the frogs in the two groups were capable of ingesting food material of similar bulk, it was decided for the purpose of investigation into the diet to treat the two years as one group.

The largest frogs which I captured in Senonches measured 91 mm., 93 mm., 98 mm., 104 mm. (females) and 84 mm. (male), whilst the largest captured in Europe as recorded by Boulenger (1897) measured 85 mm., 100 mm., 104 mm., and 125 mm. (females), and 95 mm. (male).

The essential factor to be observed when considering the diet of an anuran species is the recognition that there is a limit to the size of food items that can be ingested, varying according to the size of the individual frog and the jaw span. For this reason the diets of recently metamorphosed frogs and more mature frogs are treated separately in view of the greater limitations imposed upon the former.

2. *Stomach analysis of sixteen recently-metamorphosed frogs*

Very little specific identification of the contents was possible.

COLEOPTERA

A total of nine adults and a single larva were found in seven stomachs; of these insects four adults and the larva were so much digested that identification was impossible. The identified contents were two specimens of *Apion* sp. (Fam. Curculionidae), and single specimens of *Propylea quatuordecimpunctata* (L.), *Micraspis sedecimpunctata* (L.) (Fam. Coccinellidae) and an unidentified species (Fam. Carabidae).

HEMIPTERA

Only four specimens were found in three stomachs. These consisted of three specimens Fam. Hydrometridae and one specimen Fam. Cercopidae.

DIPTERA

Twelve adult insects were represented in seven stomachs.

COLLEMBOLA

At the water's edge, where there was a region of rotting vegetation, Collembola were plentiful and no less than 225 specimens were present in six stomachs. In one stomach as many as fifty-six specimens were found.

HYMENOPTERA

Ten stomachs contained twelve specimens of which six were ants (Fam. Formicidae).

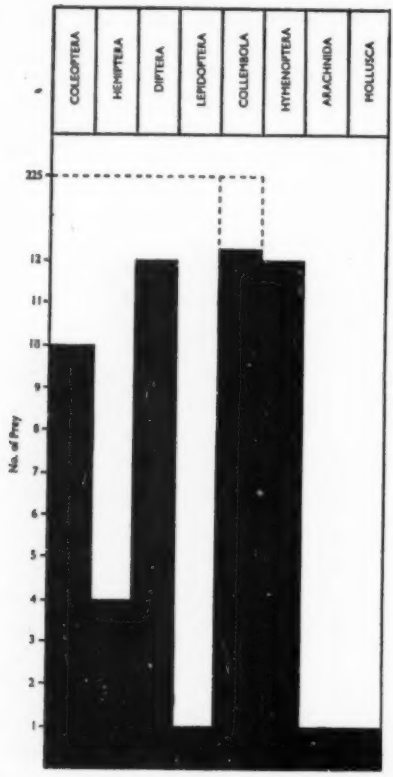


Fig. 3.—Stomach contents of sixteen recently-metamorphosed frogs.

Other food material present

One lepidopterous larva, a single mollusc and an immature male araneid (Fam. Linyphiidae) were found in separate stomachs. Two flowers (*Polygonum amphibium*) and small quantities of grass were also found.

3. *Stomach analysis of forty-seven older frogs*

Langley (1880) found that a small earthworm was digested by a frog in somewhat less than twenty-four hours and if several were ingested, the time taken to digest them was much longer. Holmes (1906) suggests that body temperature is the important factor determining the rate of digestion.

For reasons mentioned earlier in this paper the majority of the mature frogs upon which this analysis of stomach contents is based were captured late at night, and the examination of specimens and preservation of food material frequently continued until 2.0 a.m. Since it is highly probable that a longer time is involved in the digestion of chitinous prey than soft-bodied annelids, it is presumed that the stomach contents had accumulated over

a considerable period. Much of the food material was therefore so much digested as to make specific identification impossible.

COLEOPTERA

In twenty-three stomachs were sixty adult beetles and six larvae. Three of the larvae and thirty-one of the adults were *Galerucella* sp. (Fam. Chrysomelidae). The remaining larvae and nine of the adults were entirely unidentifiable. The other specimens were identified as follows: Carabidae—one *Pseudophonus rufipes* (Degeer) and eight other specimens of this family. Coccinellidae—two *Hippodamia tredecimpunctata* (L.), one *Anisosticta novemdecimpunctata* (L.), Curculionidae—one *Apion* sp. and seven other members of this family.

HEMIPTERA

From thirty-two stomachs were recovered 116 specimens of which ninety-one were Fam. Hydrometridae, seventeen Fam. Aphidiidae, two Fam. Corixidae, five Fam. Naucoridae and one other unidentified specimen.

DIPTERA

Twenty-nine stomachs contained seventy-seven specimens.

THYSANOPTERA

A single stomach contained three specimens.

LEPIDOPTERA

Fifteen stomachs contained twenty-seven specimens of which twenty-four were larvae. Of these larvae three were specimens of *Phalera bucephala* (L.) measuring 23, 39 and 40 mm. respectively found together in one stomach. (Larvae of this species were found in large numbers upon several trees surrounding the water.)

ORTHOPTERA

Six specimens of grasshoppers (Fam. Acrididae) were recovered from four stomachs.

COLLEMBOLA

A total of twenty-six specimens was recovered from five stomachs. One stomach alone contained sixteen specimens.

HYMENOPTERA

From thirty-three stomachs ninety-nine specimens were recovered. These consisted of twenty-four Fam. Formicidae (Ants), fifty-six Fam. Apidae (Bees), two Fam. Vespidae (Wasps) and seventeen other specimens.

ZYGOPTERA

Eight stomachs each contained single specimens of Damsel-Flies.

EPHEMEROPTERA

A single May-fly larva was recovered.

ACARINA

Sixteen specimens were recovered from four stomachs. These consisted of one specimen of *Trichoribates trimaculatus* Koch and fifteen unidentified water mites (Hydracarina).

MOLLUSCA

Three stomachs contained a total of seven snails.

ANURA

Ten of the stomachs examined were found to contain the partially digested remains of thirteen young frogs presumed to be *R. esculenta*.

URODELA

Two stomachs each contained the remains of an immature newt. Both newts were too much digested to make specific identification possible.

PISCES

Two young carp (*Suprimus carpus*) measuring 42 mm. and 44 mm. in length were found together in the stomach of a female frog 83 mm. in length. These fish had each been ingested head first and together represented the largest bulk of food material recovered from the stomach of any frog.

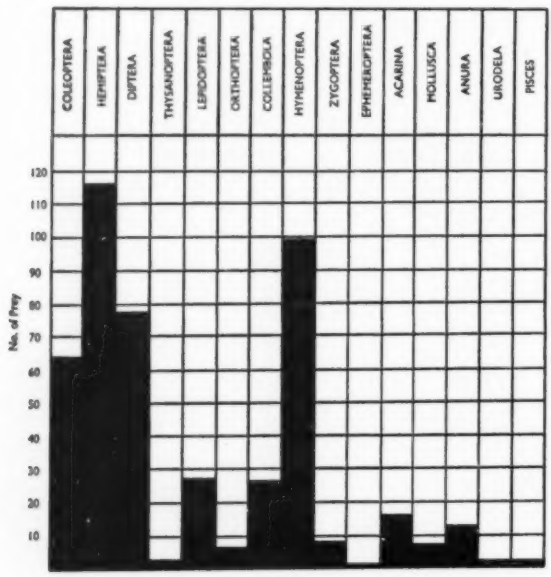


Fig. 4.—Stomach contents of forty-seven older frogs.

Other material present

Quantities of grass were found in all but two of the stomachs examined and 139 flowers (*Polygonum amphibium*) were found in twenty-four stomachs.

As many as 24, 15, 11, 10 and 8 were found in the stomachs of individual frogs.

At first glance it might appear that the flowers had fallen upon the surface of the water and, were there automatically ingested by a frog which was close by. This explanation would account for the presence of small numbers found occasionally in stomachs, but it is apparent that they were frequently ingested in large numbers and, what is more important, were found in various stages of digestion in several of the ilea examined. Similarly the presence of grass and other fragments of plant material may well be explained as inadvertantly ingested with food, but it is difficult to imagine as much as 600 mm. of grass, found in a single stomach, as being anything but ingested intentionally.

Observations upon feeding habits

Well camouflaged for an aquatic habitat, the mature Edible Frog hides amongst the vegetation and, unlike many frogs, lies in wait for prey and does not appear to forage for food.

Smith (1951) states that *Rana esculenta* feeds upon land but, during the period to which this paper refers, I did not observe a single frog from the colony of several thousands leave the water, and I watched for a period of six hours at a time to ascertain that this was so. Holmes (1934) and Angel (1946) both describe this species as being decidedly aquatic and, in the ideal habitat, only occasionally leaves the water during amplexus. The stomach contents confirm that *R. esculenta* feeds whilst in aquatic surroundings. I believe that the frogs upon which Smith based his observations were living in a canal devoid of weed and were forced to venture upon land because of the sparseness of insect food.

In the majority of frogs, the capture of small insects is accomplished by the rapid protrusion and subsequent retraction of the tongue. It is therefore interesting to note that, in the natural state, *Rana esculenta* jumps forward immediately after protrusion of the tongue, probably thus lessening the prey's already slim chances of escape. When the selected prey consists of a young batrachian or large insect the tongue plays little part in the capture for, with a sudden burst of speed, the prey is firmly grasped between the jaws and is then pushed into the buccal cavity by the forelimbs.

Distribution in relation to temperature

After several nights of capturing frogs with lights it became apparent that there was some relationship between the air temperature and the distribution and number of frogs, in groups, according to their respective sizes, throughout the swamp. On certain nights, the large mature frogs of approximately 75–95 mm. body length were predominant in the shallows at the edge of the swamp, whilst on other nights it was possible to observe hundreds of small, recently metamorphosed frogs (20–30 mm.) together with a few in the 45–70 mm. group to a mere half-dozen mature frogs.

I therefore decided to mark out areas of water at the edge of the swamp (approximately 30 feet $\times$ 30 feet) with staves, and attempted to estimate the population densities according to the number of individuals in each size-group

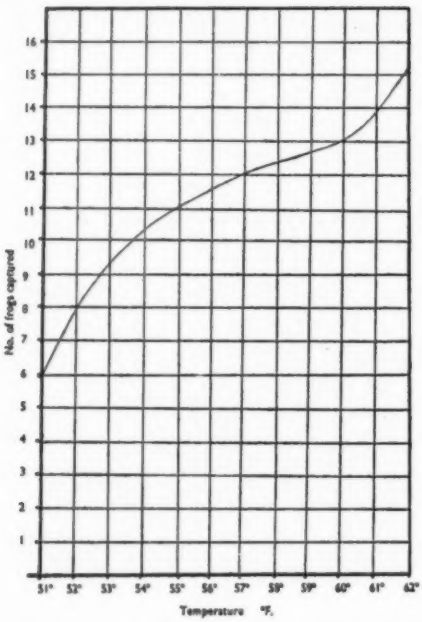


Fig. 5.—Relationship between the number of frogs captured and the air temperature.

present, and to correlate these data with the air temperature and relative humidity readings recorded with a whirling hygrometer. Observations based upon twenty counts are shown in Table 2.

TABLE 2

Air temperature at time of capture	Number of frogs observed	
	20–30 mm. & 45–70 mm. size groups	75–95 mm. size group
Greater than 57° F. (14° C.)	6	100
Less than 57° F. (14° C.)	100	1

These figures were obtained from approximately twenty test areas which were selected at random on several evenings. Whilst it is not claimed that they are 100 per cent accurate, since a diffuse weak light was used for the counts to prevent the frogs from being disturbed and therefore submerging, the remarkable differences between the numbers in the groups at above or below 57° F. remains when allowance has been made for experimental error under difficult conditions.

There are several hypotheses which could explain this phenomenon, but the main reason seems to be connected with the cannibalistic tendencies exhibited by mature adults.

As mentioned earlier, the smallest mature adult in whose stomach a recent metamorphosed *Rana esculenta* was found, measured 72 mm. in body length, and is thus regarded as being in its third year of life. The three groups of sizes represent those to be regarded as being potential prey (less than 30 mm.); those capable of being predators (greater than 70 mm.), and those which, whilst too large to be devoured, have yet an insufficiently large jaw span to be capable of devouring others (45–70 mm.). It is quite reasonable to assume that the potential prey are capable of taking evasive action and therefore swim away from the region of the swamp in which the mature frogs are present.

Water temperatures of up to 85° F. were recorded at the edge of the water during the daytime and, over a period of six or seven hours would fall by approximately 30° F. The water in the centre of the swamp, however, being much deeper, was liable to less fluctuation and, at night, the surface temperature was as much as 8° F. warmer than at the edge.

From the manner of feeding observed it would appear unlikely that a mass movement of mature frogs is based solely upon their cannibalistic tendencies but, more likely, as a definite thermotactic response.

DISCUSSION

A comparison of individual frogs captured under identical conditions frequently revealed marked differences in the prey selected. An excellent example of this phenomenon is illustrated by two recently metamorphosed frogs captured together in an area where *Collembola* were abundant and equally available to each frog yet, whilst fifty-six specimens were found in the stomach of one, there was none in the stomach of the other. Similarly the acceptance of aposematic prey was very much dependent upon the individual. No less than twelve ants were present in one particular frog, whilst no more than two specimens were found together in any of the other sixty-two stomachs examined. Many authors have stated that frogs and toads avoid or reject ants, bees and wasps, and Noble (1924) found only eleven bees and wasps amongst 6387 food animals recovered from 595 frogs and toads examined. It is therefore most interesting to note that, although alternative prey was abundant, no less than fifty-eight bees and wasps and thirty ants were eaten by thirty-three of the sixty-three *R. esculenta* examined.

Experiments with *Bufo bufo bufo* led Cott (1936) to conclude that acceptance or refusal of hive-bees depends upon the previously acquired individual experience of the toads; that there is no instinctive avoidance of unpalatable food, and that individual toads appear to differ widely in intelligence and rate of learning. Applying these conclusions to explain the presence of the fifty-six bees recovered from *R. esculenta* it seems likely that, in the natural habitat, bees are not available in sufficiently large numbers to enable anything but a small minority of frogs to learn by experience to avoid them.

Habit formation under experimental conditions is rapidly acquired but not permanently retained (Schaeffer, 1911), and a period of inclement weather inhibiting the flight of bees could well have caused the situation where few, if any, of the frogs remembered to avoid them so that bees formed a substantial porportion of the diet of this species.

From a consideration of the diverse food items recovered and observations upon the feeding habits, I conclude that there is no evidence that *R. esculenta* as a species is selective in its food habits, although individual frogs may perhaps be so.

ACKNOWLEDGMENTS

I wish to acknowledge the interest and inspiring enthusiasm of the late Mr A. D. Peart with whom this was to have been a joint paper, and the assistance in the capture of specimens in Senonches rendered by Mr P. J. Ratcliff.

My thanks are also due to Miss J. E. Tanfield (Kingston Technical College) and Mr E. T. Hurlock for their assistance and encouragement, and to the late Dr Malcolm Smith (British Museum, Natural History), for invaluable advice.

I am indebted to Mr E. T. Bezant and Mr D. C. Drummond (Ministry of Agriculture, Fisheries and Food), Dr A. M. Hughes (Royal Free Hospital School of Medicine), Dr G. Taylor (Royal Botanic Gardens, Kew) and Mr G. Palmer (British Museum, Natural History) for the identification of the Arachnida, Coleoptera (*Galerucella* sp.), Acarina, flowers and fish respectively.

SUMMARY

Sixteen recently metamorphosed and forty-seven mature frogs were captured and the stomach contents examined. In view of the more limited choice of available prey imposed upon the former, due to the smaller jaw span, it was decided to tabulate the contents separately.

Aposematic prey formed a substantial proportion of the diet.

Large numbers of flowers were recovered from several stomachs.

Specific choice of prey varied with the individual, and it was concluded that *R. esculenta* as a species is not selective.

In the natural habitat *R. esculenta* does not by choice leave the water to feed unless there are insufficient aquatic prey.

It was found that mature adult frogs showed cannibalistic tendencies and this, coupled with a thermotactic response, influenced their distribution within the habitat.

REFERENCES

Angel, F. (1946). Reptiles et Amphibiens. *Faune de France* no. 45.

Boulenger, G. A. (1897). *The tailless batrachians of Europe*, **1**. London: Ray Society.

Cott, H. B. (1932). On the ecology of tree-frogs in the Lower Zambesi valley with special reference to predatory habits considered in relation to the theory of warning colours and mimicry. *Proc. zool. Soc. Lond.* **1932**, 471–541.

Cott, H. B. (1936). The effectiveness of protective adaptations in the hive-bee, illustrated by experiments on the feeding reactions, habit formation and memory of the common toad (*Bufo bufo bufo*). *Proc. zool. Soc. Lond.* **1936**, 111–33.

COTT, H. B. (1957). *Adaptive coloration in animals.* London: Methuen.

DRAKE, C. J. (1914). The food of *Rana pipiens* Schreber. *Ohio Nat.* **14,** 257–69.

HOLMES, S. J. (1906, 1934). *The biology of the frog.* New York: Macmillan. [4th edition, 1934]

LANGLEY, J. N. (1880). On the histology and physiology of the pepsin-forming glands. *Phil. Trans.* **172,** 663–711.

LIU, CHI-YING, and CHEN, KAN-FAN (1932). Analysis of the stomach contents of two species of frogs (*Rana limnocharis* and *Rana nigromaculata*) in the vicinity of Kashing with special reference to insects. *Yearbook Bur. Ent. Hangchow* **2,** 183–91.

NEEDHAM, J. G. (1905). The summer food of the bull-frog (*Rana catesbiana* Shaw) at Saranac Inn. *Bull. New York State Mus.* **86,** 9–15.

NOBLE, G. K. (1918). The amphibians collected by the American Museum Expedition to Nicaragua in 1916. *Bull. Amer. Mus. nat. Hist.* **38,** 311–47.

NOBLE, G. K. (1924). Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition 1909–15. Part III. *Bull. Amer. Mus. nat. Hist.* **49,** 147–347.

PARKER, H. W. (1930). A collection of frogs from Portuguese East Africa. *Proc. zool. Soc. Lond.* **1930,** 897–905.

SCHAEFFER, A. A. (1911). Habit formation in frogs. *J. Anim. Behav.* **1,** 309–35.

SMITH, M. (1951). *The British amphibians and reptiles.* London: Collins. (Revised edition 1954).

SMITH, M. (1952). The climate of the British Isles and its influence on the habits and distribution of the amphibians and reptiles. *Brit. J. Herpet.* **1,** 103–11.

SMITH, M. (1953). The feeding habits of the marsh frog (*Rana ridibunda ridibunda*). *Brit. J. Herpet.* **1,** 170–72.

WITTE, G .F. DE (1948). Amphibiens et Reptiles. *Faune de Belgique, Bruxelles.* Musée, Royal d'Histoire de Belgique.

A NEW SPECIES OF *EUKROHNIA* FROM THE SOUTHERN OCEAN WITH A NOTE ON FERTILIZATION

BY

P. M. DAVID

National Institute of Oceanography

[Communicated by Dr. N. A. Mackintosh, C.B.E.—Accepted 15 April 1958]

(With 3 figures in the text)

CONTENTS

	Page
Introduction	597
Methods	597
Synonymy and description of the species	598
Discussion	598
Distribution	603
Key	604
Fertilization	604
Summary	605
References	605
Appendix	606

INTRODUCTION

In the course of my work on the Discovery chaetognath collections I had occasion to compare, side by side, specimens of deep living *Eukrohnia* from the Southern Ocean and from the North East Atlantic. Certain points of difference were immediately apparent, and further examination has shown that the Southern Ocean form should be regarded as a separate species. This species is very similar to *Eukrohnia fowleri* R. Zahony and had been regarded as such by members of the Discovery staff for some years. It is however in some respects closer in appearance to the large form of *E. hamata* which is common in the coldest waters of the Southern Ocean and may possibly be equally related to this form and *E. fowleri*. Among the specimens examined were some which seemed to shed some light on the mode of fertilization in this species.

METHODS

The material examined had all been preserved in neutral sea water formalin and was in good condition. A few specimens were examined alive in 1950 and 1951 but since at that time I regarded them as *E. fowleri*, no particular note was made apart from a colour sketch of one of them.

Weak methylene blue was used for staining to show the fins and eyes. The figures shown here being drawn on squared paper with the use of a micrometer eyepiece.

SYNONYMY AND DESCRIPTION OF THE SPECIES

EUKROHNIA BATHYANTARCTICA, sp. n.

E. fowleri Ritter Zahony 1911 (part).
Eukrohnia sp. David 1958.

Holotype. A specimen 25·9 mm. long taken in a 2 m. net (TYF) which fished between 2400 and 1150 m. at Discovery station 1639, 58°35′S., 92°06′2E. on 2. xii. 35.

Registration number. British Museum (Nat. Hist.). 1958 : 6 : 2 : 34.

Body proportions. Total length 25·9 mm. (26·6 mm. including caudal fin), tail segment 6·0 mm., 23·2 per cent of total length.

Head armature. Hooks 12 and 13, teeth 11 and 12.

Gonads. Tail segment full, but vesicles apparently damaged, ovary 1·3 mm. 5·0 per cent of total length, eggs small, remnants of spermatophores protruding from both oviducts.

Paratypes. Ten specimens taken in a 2 m. closing net fished from 2400-1150 m. at Discovery station 1639, 58° 35′ S., 92° 06′ 2 E., on 2. xii. 35.

Registration numbers. British Museum (Nat. Hist.). 1958 : 6 : 2 : 35/44.

The range of variation in the characters listed below is that found in 50 specimens from Stations 1939 and 2812. See appendix p. 606.

Characters

Fins. Commence at ventral ganglion and extend on to the tail segment for about one-third of its length.

Tail. Broad, 19·3 to 25·0 per cent of body length.

Teeth. Up to 16.

Hooks. Up to 14.

Seminal vesicles. Shape is not known but is probably ovoid, they are situated close to the lateral fins.

Ovaries. Short, even when fully mature.

Collarette. Absent.

Corona. Shape not known.

Length. Up to 31 mm.

Distribution. Probably an " endemic " antarctic species, always lives below 1000 m.

DISCUSSION

From Table 1 it can be seen that *E. bathyantarctica* and *E. fowleri* differ in six features. Three of these are trivial and quite possibly are not real differences but are due to the small numbers of *E. bathyantarctica* which have been examined. Thus the difference in maximum size, the difference in tail segment percentage and difference in the numbers of hooks are so slight that they cannot be regarded as significant.

On the other hand the other three characters, the teeth, the eyes, and the presence of a " collarette " like structure, seem to be diagnostic. Fig. 1 shows a comparison of teeth numbers plotted against total length for the two species and is based on forty-eight specimens of *E. bathyantarctica* and eighty specimens of

E. fowleri from the Atlantic (from Ritter-Zahony, 1911). It is evident that there is no overlap in teeth numbers in these two species. There is in fact a considerable gap at all lengths, and as the data in the figure cover a wide range of size and age in both species one of Tchindonova's (1955) objections to the use of teeth numbers for specific determination would appear to be adequately answered. As to her other objection, that differences in teeth numbers are due to "ecological intra-species variations", one can only observe that each species occupies a very similar, if not identical, ecological niche, and that if their distribution should prove to overlap, they would certainly be found to be occupying the same vertical horizon. One can therefore I think regard the difference in teeth numbers in this case as a good taxonomic character.

TABLE 1.

A comparison of various diagnostic features in *E. bathyantarctica* and related species.

Features	*E. bathyantarctica*	*E. fowleri*	*E. hamata*
Total length	to 31 mm.	to 40 mm.	to 43 mm.
Fins	[from ventral ganglion on to about one-third of tail segment]		
Tail segment	19·3–25·0% LT	21·0–27·0% LT	19·0–24·0% (31·0% Fraser 1952) LT
Hooks	to 14	to 13	to 9
Teeth	to 16	to 30	to 23 (25 Fraser 1952)
Seminal vesicles	probably ovoid	not yet described	elongated ovoid
Ovaries	short and stumpy	short and stumpy	extend to about half the length of the body segment at full maturity.
Corona	?	Pear shaped	Pear shaped
Eyes	Without pigment fleck	With pigment fleck	Without pigment fleck
Gut	Brick red	Brick red	Colourless
Depth distribution	Below 1000 m.	Below 750 m.	Surface to 1500 m.
Other features	(a) No "collarette" at ventral ganglion	"Collarette" at ventral ganglion	No "colarette" at ventral ganglion.
	(b) Remnants of seminal vesicles project from oviduct after fertilisation	Remnants of seminal besides project from oviduct after fertilisation	No remnants of seminal vesicles project from oviducts.

There are however, two more, quite reliable, anatomical differences. Ritter-Zahony (1911) in his description of *E. fowleri* (his first description in 1909 is little more than an announcement of the name) emphasised the presence of a pigment fleck in the eye as an important feature, and it has certainly been present in all the specimens of *E. fowleri* I have examined. In *E. bathyantarctica* on the other hand I have been quite unable to find any trace of a pigment fleck, and indeed the specimens usually needed to be stained before even the outline of the eyes (Fig. 3 b) was visible.

In *E. fowleri* there is a structure rather reminiscent of the foamy collarette of *Pterosagitta draco* which covers the region of the ventral ganglion (Fig. 2 b). It is more extensive on the dorsal than on the ventral surface and appears to consist of large clear thin-walled vacuoles whose polygonal shape (Fig. 3 d)

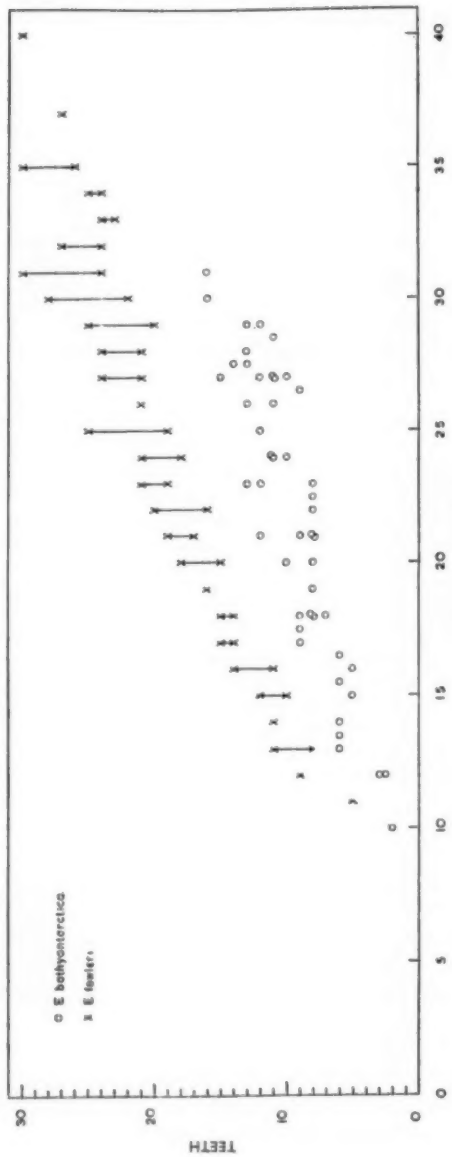


Fig. 1.—The numbers of teeth of *E. bathyantarctica* and *E. fowleri* plotted against total length. The data for *E. fowleri* have been taken from Ritter-Zahony (1911) and those for *E. bathyantarctica* are from 48 specimens in the Discovery collections.

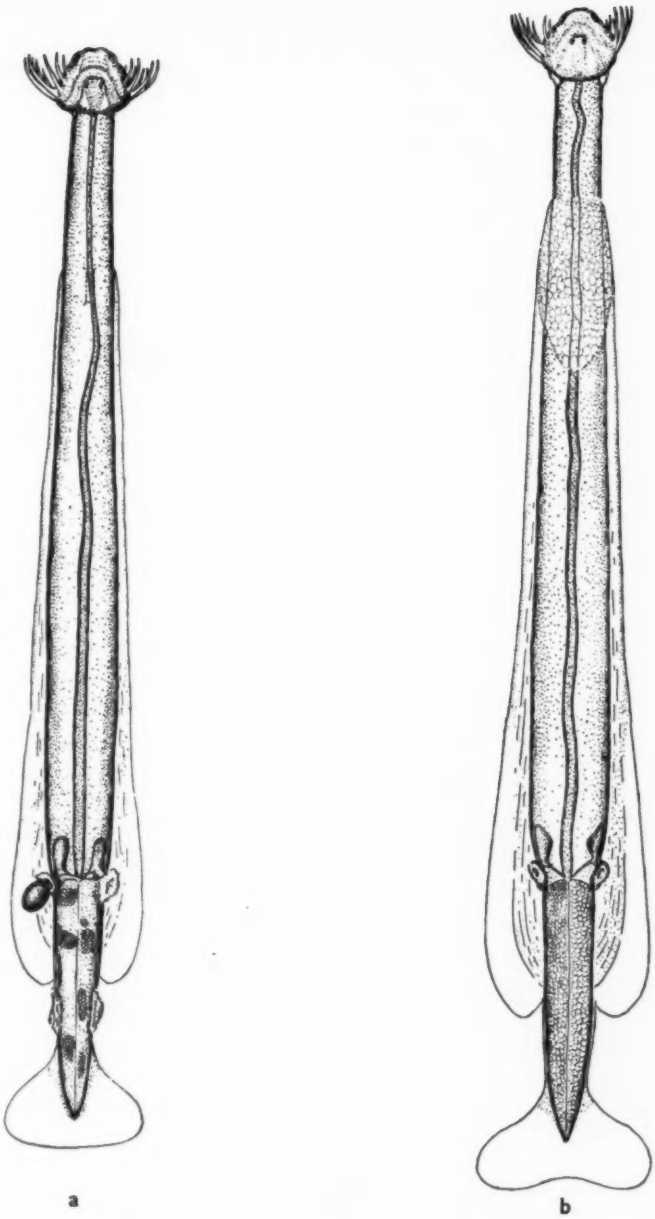


Fig. 2.—(a) *E. bathyantarctica*. (b) *E. fowleri*.

seems to be due to their being closely packed together. There is no collarette in the region of the neck, which is where it is most usually found, the structure somewhat resembling a collarette at the neck in Fig. 3 a being in fact a fold of the epidermis caused by the position of the head muscles at preservation.

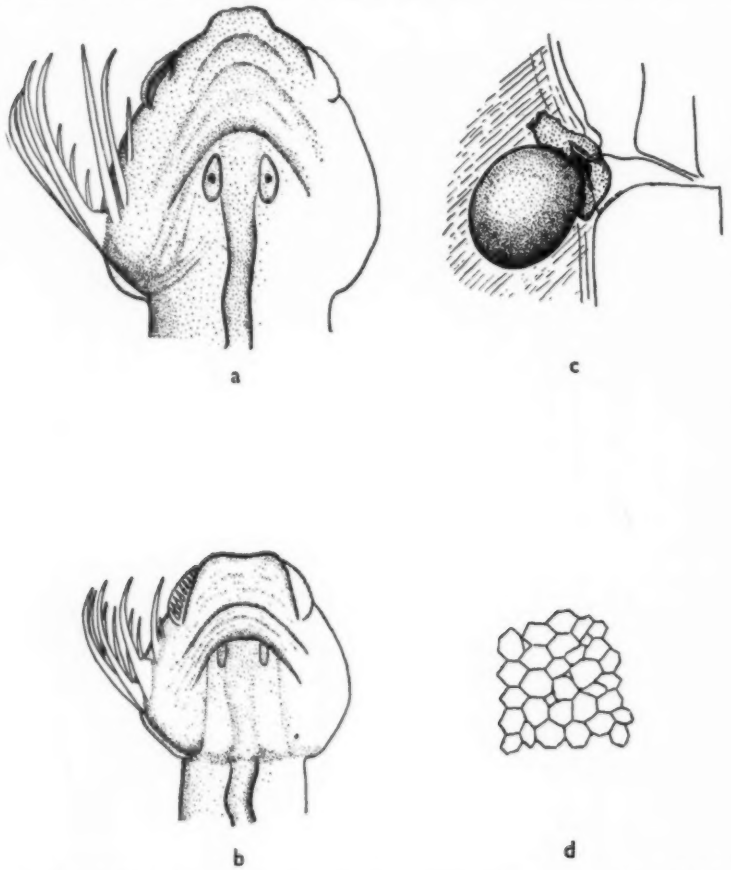


Fig. 3.—(a) Head of *E. fowleri*. (b) Head of *E. bathyantarctica*. (c) External opening of the oviduct of *E. bathyantarctica*. (d) Part of the " collarette " of *E. fowleri*.

It is perhaps surprising that the " collarette " at the ganglion has not been previously reported in *E. fowleri*. However Burfield & Harvey (1926) have reported it in *E. richardi*, a species which is almost certainly synonymous with *E. fowleri*.* Fraser (personal communication) informs me that he has

*I have noticed that if a plankton sample containing *E. fowleri* remains for several hours in a warm laboratory before preservation, a number of specimens having the body proportions of *E. richardi* will be found after preservation, due it seems to contraction of the longitudinal muscle of *E. fowleri* when permitted to die slowly. The green colour of *E. richardi* reported by Germain and Joubin 1916 must, I think, have been caused by some form of unintentional chemical staining.

frequently observed it in Arctic and N. Atlantic specimens of *E. fowleri* but that it is often more or less damaged in the net.

Comparison with *E. hamata* shows that in size, tail segment percentage, and fins the three species are virtually identical. The teeth numbers of *E. hamata* are intermediate between the two other species but the number of hooks is consistently smaller and is probably the most certain taxonomic difference. In addition the hooks in *E. hamata* are more solid and robust than those of the other two species. In mature specimens of *E. hamata* the ovaries often extend to half the length of the body segment whereas in the other species they seldom attain more than three or four millimetres in length.

The eyes of *E. hamata* like those of *E. bathyantarctica* are without pigment. The gut is colourless in *E. hamata*, and although the red pigment on the gut in *E. fowleri* and *E. bathyantarctica* (as also in *Sagitta macrocephala* and *Heterokrohnia mirabilis*) fades after some years of preservation and exposure to light, the granular opaque appearance of the gut walls in these species is always sufficiently conspicuous to distinguish them from species without pigment. Tokioka (1939) has reported specimens of *E. hamata* with pigment in the gut, two at least of which appear to have been very like *E. fowleri* or *E. bathyantarctica*, but it is not possible to know if the pigmentation was the faint reddish stain which can emanate from red crustaceans in the gut or the opaque orange-red layer which surrounds the gut of *E. fowleri* (and other species).

In depth distribution *E. hamata* is an epiplanktonic form in cold waters, and has an extensive vertical range, while of the other two species *E. fowleri* is seldom found above 750 m. and *E. bathyantarctica* never above 1000 m, both being most common below 1500 m. and probably extending to more than 3000 m.

E. hamata resembles *E. bathyantarctica* in that it has no " collarette " in the region of the ganglion. Both *E. fowleri* and *E. bathyantarctica* have, when mature, the remnants of the seminal vesicles projecting from the funnel shaped external opening of the oviduct, but I have never seen these in *E. hamata*.

DISTRIBUTION

The Discovery collections do not contain sufficient deep samples from Subantarctic and Antarctic waters to define the limits of horizontal distribution of *E. bathyantarctica* or the southern limits of that of *E. fowleri*. *E. fowleri* has been considered as a cosmopolitan form of all deep oceans including the Antarctic and I have examined specimens from the North Atlantic, the Arctic, the equatorial Indian Ocean, the Peru current and the Subtropical regions of the South Atlantic and S.W. Pacific Oceans, which all seem to agree closely with the published descriptions of the species. However I have not seen any specimens taken from south of the Subtropical convergence, and south of the Antarctic convergence only *E. bathyantarctica* has been found.

Only a small number of deep samples from the Antarctic have been examined for *E. bathyantarctica* and its circumpolar range is almost certainly more extensive than the list of records suggest. It has been found at the following stations.

Date	Station	Position		Net	Depth m.	No. of specimens
2. xii. 35	1639	58° 35′ S.	92° 06·2′ E.	TYFB	2400–1150	88
17. iii. 36	1702	64° 20·1′ S.	139° 54′ E.	TYFB	2000–1250	118
30. iii. 36	1727	54° 32·2′ S.	106° 25′9 E.	N7OV	1500–1000	1
3. vi. 36	1782	58° 44·6′ S.	00° 01·5′ E.	N7OV	1500–1000	1
25. iii. 37	2015	59° 23·8′ S.	00° 09·3′ E.	N7OV	1500–1000	1
15. viii. 38	2389	52° 35·3′ S.	00° 04·5′ E.	N7OV	1500–1000	1
17. viii. 38	2393	56° 42·3′ S.	00° 38·3′ E.	N7OV	1500–1000	2
20. ii. 51	2812	64° 53· S.	89° 54′ E.	N7OV	2000–1500	4
9. vii. 51	2852	57° 35′ S.	37° 20′W.	N7OV	1500–1000	1

KEY

	One pair of lateral fins, one paired row of teeth ..... genus	*Eukrohnia*
1.	More than ten hooks ; gut pigmented	2.
	Less than ten hooks ; gut not pigmented	*E. hamata.*
2.	Eyes with pigment fleck ; teeth up to 30	*E. fowleri.*
	Eyes without pigment fleck ; teeth up to 16	*E. bathyantarctica.*

FERTILIZATION

Specimens of *E. fowleri* and *E. bathyantarctica* are frequently found to have peculiar structures apparently attached to the funnel shaped external opening of the oviduct. These structures consist of thin transparent material and in form resemble an inverted tulip. Specimens in which this structure was present were usually found to have short stumpy ovaries and it has been suggested by *Tchindonova* (1955) that the structures, in *E. fowleri*, are ruptured "ovarian sacs". Among a collection of *E. bathyantarctica* taken at station 1639 was one specimen (Figs. 2 a, and 3 c) in which there was an egg-shaped opaque structure appended to one oviduct. With a low power binocular it could be seen that the structure was attached by a fine tube which ran directly into the oviduct. Examination of the usual "ruptured sac's" showed that they too were each attached by a fine tube, and it was concluded that they represented a later stage of the opaque egg-shaped structure. I have not been able to find a single specimen of either *E. fowleri* or *E. bathyantarctica* with mature seminal vesicles, but this opaque structure seemed to be of the right size and shape to have fitted where the areas of ruptured epithelium on the tail segment in a number of specimens showed the seminal vesicles to have been, and it seemed probable that the structure, and the "ruptured sacs" attached to the oviduct were seminal vesicles and their remains which had in some unknown way been transferred from the tail segment of one animal to the oviduct of another. If this supposition is correct then the fine tube which enters the oviduct is probably the vas deferens whose normal function in chaetognaths is to transfer the sperm from the tail segment to the seminal vesicles. In the two species considered here they must also work in a reverse direction and transfer sperms from the vesicle to the ovary. Although little is known of the methods of pairing and fertilization in chaetognaths (except in *Spadella* where the process has been most beautifully described and photographed by Ghirardelli 1954) there does not seem to have been any suggestion

so far that the seminal vesicles might act as spermatophores or the vas deferens as an intromissive organ.

Serial sections were made of one specimen of *E. bathyantarctica* with a view to elucidating the path of the tube in the lumen of the oviduct, but as Professor Ghirardelli, who is at present writing a monograph on fertilization in the Chaetognatha, has agreed to make a study of these specimens it was felt that the investigation would be far better left in his capable hands rather than that I should myself launch out into an unfamiliar field.

SUMMARY

A new species of the genus *Eukrohnia*, *E. bathyantarctica*, is described ; it is a deep living form, so far only found in the Southern Ocean. It resembles both *E. fowleri* and *E. hamata* in many features. Evidence is given which suggests that in this species, and also in *E. fowleri* the seminal vesicles function as spermatophores and are attached intact to the external opening of the oviduct by a fine tube which is probably the vas deferens.

REFERENCES

Burfield, S. T. & Harvey, E. J. W. (1926). Chaetognaths from the Percy Sladen Trust Expedition. *Trans. Linn. Soc. Lond.* Ser. 2, **19,** 93–199.

David, P. M. (1958). The distribution of the Chaetognatha of the Southern Ocean. *Discovery Rep.* **29,** 199–228.

Fraser, J. H. (1952). The Chaetognatha and other zooplankton of the Scottish area and their value as biological indicators of hydrological condition. *Marine Res.* no. 2, 1–52.

Germain, L. & Joubin, L. (1916). Chetognathes provenants des campagnes des Yachts "Hirondelle" et "Princesse Alice" 1885–1910. *Result. Camp. sci. Monaco* **49,** 1–118.

Ghirardelli, E. (1954). Sulla biologia della riproduzione in *Spadella cephaloptera* Busch (Chaetognatha). *R. C. Acad. Sci. Ist. Bologna, Cl. Sci. Fis. Ann.* 242, Ser. 11, **1,** 1–19.

Ritter-Zahony, R. (1909). Die Chatognathen der Gazelle-Expedition. *Zool. Anz.* **34,** 787–93.

Ritter-Zahony, R. (1911). Revision der Chaetognathen. *Deutsche Sudpolar-Exped.* **13** (5), 1–71.

Tchindonova, J. G. (1955). Chaetognatha of the Kurile-Kamchatka Trench. *Trudy Inst. Okeanol.* **12,** 298–310.

Tokioka, T. (1939). Chaetognatha collected chiefly from the Bays of Sagami and Suruga with some notes on the shape and structure of the seminal vesicle. *Rec. Oceanogr. Wks. Jap.* **10,** No. 2, 123–50.

APPENDIX

Eukrohnia bathyantarctica

Length	Tail seg Percentage	Hooks	Teeth	Length	Tail seg Percentage	Hooks	Teeth
31	22·6	13	16	22·5	22·2	13	8
30	21·6	13	16	22	19·3	13	8
29	24·1	13	13	21	20·2	12	8
29	24·0	12	12	21	—	13	8
28·5	23·2	14	11	21	—	12	12
28	22·3	13	13	21	—	12	9
27·5	23·1	12	14	20	21·2	12	8
27·5	22·8	14	13	20	—	12	10
27	24·0	12	11	19	—	12	10
27	—	13	11	18	25·0	12	8
27	22·4	14	12	18	—	12	9
27	—	13/14	10	18	—	13	7
27	—	13	15	18	—	12	8
26·5	24·0	14	16	17·5	—	12	9
26·5	—	13	9	17	25·0	13	9
26	23·0	12	11	16·5	24·2	13	6
26	23·0	13	15	16	25·0	13	5
25	23·0	12	12	15·5	22·6	12	6
25	22·7	14	12	15	—	12	5
24	21·9	12	10	14	23·2	12	6
24	—	12	11	13·5	—	11	6
24	—	13	11	13	—	11	6
23	21·7	11/12	8	12	25·0	11	3
23	—	12	14	12	20·9	12	2/3
23	—	11	12	10	25·0	12	2

VARIATION IN THE MAXILLARY NERVE OF CERTAIN MAMMALS

BY

E. H. ASHTON AND C. E. OXNARD

Department of Anatomy, University of Birmingham

[Accepted 15th April 1958]

(With 3 figures in the text)

CONTENTS

	Page
Introduction	608
Materials and methods	609
Anatomical material	609
Dissection	610
Anatomical nomenclature	611
Results	611
Order : Insectivora	611
Facial features	611
Maxillary nerve	611
Exit from cranium	611
Zygomatic and lacrimal nerves	611
Dental nerves	611
Division of infraorbital nerve	613
Facial distribution	613
Order { Lagomorpha	613
Order { Rodentia	613
Facial features	614
Maxillary nerve	614
Exit from cranium	614
Zygomatic and lacrimal nerves	614
Dental nerves	614
Division of infraorbital nerve	614
Facial distribution	615
Order : Carnivora	615
Facial features	615
Maxillary nerve	617
Exit from cranium	617
Zygomatic and lacrimal nerves	617
Dental nerves	617
Division of infraorbital nerve	617
Facial distribution	618
Order { Perissodactyla	620
Order { Artiodactyla	620
Facial features	620
Maxillary nerve	620
Exit from cranium	620
Zygomatic and lacrimal nerves	620
Dental nerves	621
Division of infraorbital nerve	621
Facial distribution	621

CONTENTS (continued)

	Page
Discussion	622
Acknowledgments	623
Summary	624
References	624

INTRODUCTION

Although varying in relative size from species to species, the major subdivisions of the maxillary nerve are, throughout the Primates, constant in their general disposition (Ashton & Oxnard, 1958). They comprise first, a zygomatic branch which leaves the main trunk soon after its emergence from the foramen rotundum ; second, twigs by which the sphenopalatine ganglion is suspended, and third, the infraorbital nerve which passes forward on the orbital floor supplying the upper teeth and finally splitting at a variable point into nasal and labial divisions. The nasal division subdivides into a superior nasal branch which ramifies on the dorsum of the nose (and in prosimians supplies the medial part of the rhinarium) and an inferior nasal branch which is distributed to the lateral part of the rhinarium and to the nasal vestibule. The labial division supplies the skin of the cheek and upper lip together with the mysticial vibrissae, some of its fibres being fasciculated with twigs of the seventh nerve to form the infraorbital plexus.

In prosimians, most of the fibres of the infraorbital nerve are distributed to the rhinarium, and in consequence, the nasal division is bigger than the labial. In monkeys, apes and man where there is no rhinarium, relatively more fibres are distributed to the facial skin, and the labial division is, in these forms, the bigger. Although in these primate groups the vibrissae are reduced progressively, any resulting decrease in the size of the labial division appears to be offset by the increased numbers of fibres that are associated with the facial nerve consequent upon a concomitant elaboration of the facial muscles. The development of the infraorbital plexus also appears to obscure any variations in the sizes of the two major divisions of the nerve that may have resulted from the presence of specialized facial features (e.g. the cheek pouches of Old World monkeys).

Correspondingly detailed information for other mammalian orders is not, to the best of our knowledge, available. No comparative studies appear to have been directed specifically towards an analysis of the branches of the maxillary nerve, and it appears that not more than brief references to their distribution are contained in the available accounts of the anatomy of various mammalian species. For instance, Stubbs (1776) in his description of the horse (*Equus caballus*) merely figures the cut end of the infraorbital nerve and mentions that it " breaks up into branches which pass to the nostrils, muzzle and lips ". More recently, Schulte & Forest Smith (1918) have noted that in the pygmy sperm whale (*Kogia breviceps*) the trunk of the maxillary nerve gives branches to various facial structures and that a small " ganglion-like formation " on the dorsum of the rostrum receives contributions from both the fifth and seventh nerves. Again Sonntag & Woollard (1925) in an extensive account

of the aardvark (*Orycteropus afer*) provide only a brief note to the effect that the maxillary division of the trigeminal is " immense ", and that on emerging on to the face it divides into various branches some of which form a plexus with the facial nerve. Other anatomical and systematic studies—e.g. that by Hines (1929) on the monotreme genus *Ornithorhynchus*—give equally little information about the maxillary nerve, while standard text-book descriptions of the anatomy of the domestic animals (e.g. Bradley, 1927 ; Ellenberger & Baum, 1894 ; Sisson, 1930) are scarcely more extensive. Even when to these sources is added the information contained in two brief studies of the zygomatic and lacrimal nerves in carnivores (Lacroix, 1926 ; Winckler, 1932), the total is insufficient to give any indication of the scale of variation in the maxillary nerve of the mammals as a whole. *A priori* this could be expected to be considerable because although, in contrast to the Primates, the group exhibits few striking variations in the complexity of the facial musculature (Huber, 1930), there exist, in connection with the vibrissae and other facial features, differences at least as great as those which affect the rhinarium and facial muscles of Primates and which are in this group correlated with considerable variations in the sizes of the nerve branches (Ashton & Oxnard, 1958).

Thus, in some instances (e.g. many carnivores), there is in the development of these facial structures, little departure from the primitive mammalian pattern (Pocock, 1914), one in which the rhinarium is prominent, and the vibrissae are arranged in well-defined groups, the most extensive (mysticial vibrissae) lying on the upper lip. In other cases (e.g. pinnipeds), the rhinarium is reduced but the mysticial vibrissae are enormously enlarged. In yet others (e.g. ungulates) it is the vibrissae that are reduced or absent, and whereas in some sections of the group (e.g. the Bovidae), the rhinarium is exceptionally prominent, in others (e.g. the Equidae) it is rudimentary, and the snout is completely covered by hairy skin.

Considerable variation also occurs in the architecture of the upper lip (Boyd, 1932 ; Osman Hill, 1948). Sometimes, as in the dog (*Canis familiaris*) the embryonic maxillary processes remain, even in the adult, widely separated, and the philtrum comprises a naked, downwardly-projecting process of the rhinarium. In others (e.g. some rodents) these processes meet in the midline, but only their deeper layers fuse, and the philtrum is divided by a sagittal groove. In the remaining groups (e.g. Equidae, Suidae), the maxillary processes fuse completely and the philtrum is confluent with the remainder of the upper lip.

The present study was undertaken to ascertain first, whether in certain non-primate mammalian orders, the infraorbital nerve splits initially into nasal and labial divisions, and second, to determine the extent to which its branches vary according to the development of different facial features, especially vibrissae.

MATERIALS AND METHODS

Anatomical material

The species studied, arranged according to the scheme outlined by Simpson (1945), are listed in Table 1.

TABLE 1

The numbers and types of specimens studied

Order	Genus & species	Vernacular name	Number of specimens
Insectivora	*Sorex araneus*	Common shrew	2
	Macroscelides rozeti	Elephant shrew	1
	Petrodromus tetradactylus	Four-toed elephant shrew	1
Lagomorpha	*Oryctolagus cuniculus*	Rabbit	6
Rodentia	*Sciurus sp.*	Squirrel	2
	Cricetus cricetus	Golden hamster	6
	Rattus sp.	Rat	6
	Mus sp.	Mouse	10
	Myocastor coypus	Coypu	1
	Dasyprocta aguti	Agouti	1
Carnivora	*Canis familiaris**	Dog	11
	Felis catus	Cat	2
	Mustela putorius	Ferret	9
	Lutra lutra	Otter	1
	Phoca vitulina	Seal	1
Perissodactyla	*Equus caballus*	Horse	4
Artiodactyla	*Bos taurus*	Cow	7
	Ovis aries	Sheep	2
	Sus scrofa†	Pig	10

*2 adults, 1 immature, 8 foetal siblings. †2 adults, 2 sets of 4 foetal siblings.
All other specimens were adult.

The material is less extensive than could be desired, consisting of representatives of only six orders of placental mammals. In some cases, (e.g. domestic animals) it was possible to obtain sufficient representatives of each species to give an indication of certain minor variations in the pattern of branching of the maxillary nerve. In others, however, (e.g. pinnipeds) only isolated specimens were available and comparison was, of necessity, restricted to major features.

Dissection

The right or left maxillary nerve was dissected from the trigeminal ganglion to the face. Note was made of :

(1) whether the ophthalmic and maxillary divisions of the trigeminal nerve left the cranium independently through a superior orbital fissure and foramen rotundum or whether they passed through a single " orbital fissure " (Winckler, 1932),

(2) whether the lacrimal nerve took origin from the ophthalmic or from the maxillary trunk,

(3) the point of origin of the zygomatic nerve and whether or not it was linked to the lacrimal nerve by an anastomotic filament,

(4) the origin of the superior dental nerves,

(5) the primary subdivision of the infraorbital trunk, and
(6) variation in the distribution of the resultant branches.

Anatomical nomenclature

The nomenclature used in this paper is, in general, that appearing in most modern textbooks of human anatomy. It has been supplemented where necessary by the additional terms defined in the earlier study of the primate maxillary nerve (Ashton & Oxnard, 1958).

RESULTS

Order : INSECTIVORA (Fig. 1)

Sorex araneus—the common shrew (two specimens)
Macroscelides rozeti—the elephant shrew (one specimen)
Petrodromus tetradactylus—the four-toed elephant shrew (one specimen)

Facial features

The snout of the shrew is exceptionally long, and is surmounted by a small, but clearly-differentiated rhinarium. In the common shrew, a fine hairy groove projecting downwards from the rhinarium divides the philtrum sagittally but in both species of elephant shrew, the philtrum is formed by a thin band of naked skin continuous above with the rhinarium. Mysticial vibrissae are, in all species developed on both the upper lip and sides of the snout. In the elephant shrew, however, there are relatively fewer vibrissae on the snout than in the common species of this animal.

Maxillary nerve

In the four specimens examined, there were no variations in the mode of exit of the maxillary nerve from the cranial cavity. The zygomatic and dental branches were also constant in their origin and distribution.

Exit from cranium

The maxillary division of the trigeminal nerve lies lateral to the ophthalmic and each subdivides while still within the cranial cavity. Their respective branches emerge through an undivided orbital fissure in two main bundles, each in its own sheath of connective tissue. The maxillary division then passes forwards on the orbital floor as the infraorbital nerve.

Zygomatic and lacrimal nerves

The zygomatic nerve arises from the maxillary trunk within the cranial cavity and enters the orbit with the lacrimal branch of the ophthalmic division. While passing laterally across the orbital floor, the zygomatic nerve gives off a fine filament which runs upwards to join the lacrimal nerve.

Dental nerves

The infraorbital nerve gives off two posterior superior dental branches which pass into separate canals in the posterior aspect of the maxilla to supply

the upper molar teeth. After the infraorbital nerve has entered the infraorbital canal, an anterior superior dental branch leaves its lateral side and passes into its own bony canal leading towards the incisor teeth.

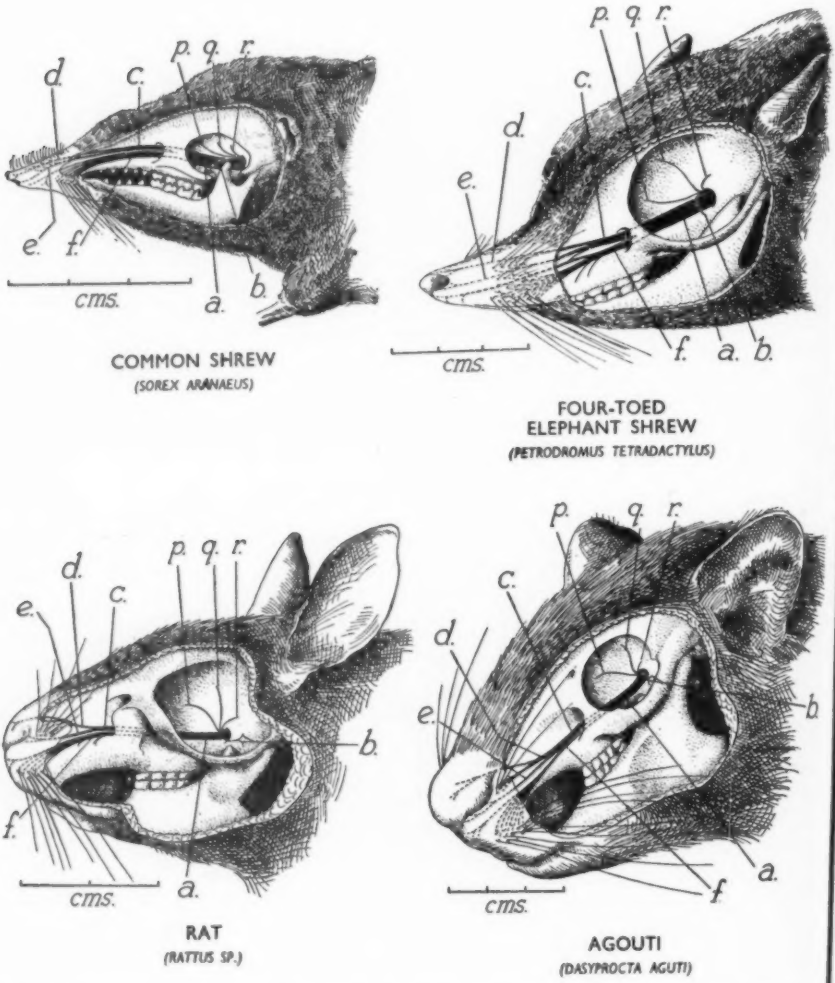


Fig. 1.—Variation in the maxillary nerve of certain insectivores and rodents. (*a*) Infraorbital nerve. (*b*) Zygomatic nerve. (*c*) Nasal division of infraorbital nerve. (*d*) Superior branch of nasal division of infraorbital nerve. (*e*) Inferior branch of nasal division of infraorbital nerve. (*f*) Labial division of infraorbital nerve. (*p*) Nasociliary branch of ophthalmic division of trigeminal nerve. (*q*) Frontal branch of ophthalmic division of trigeminal nerve. (*r*) Lacrimal branch of ophthalmic division of trigeminal nerve.

Division of infraorbital nerve

General description : The infraorbital nerve passes through the internal opening of the infraorbital canal and splits therein into nasal and labial divisions.

Variation : In both specimens of the common shrew, the labial division was appreciably bigger than the nasal. In the two available species of elephant shrew, however, the nasal division was the more prominent.

Facial distribution

General description : On emerging from the infraorbital foramen, the nasal division splits into superior and inferior branches. The first lies superficially, and after ramifying on the dorsum of the snout supplies the medial part of the rhinarium. The second lies more deeply in the soft tissues of the face, and supplies the lateral and inferior parts of the rhinarium. A few twigs from each branch are distributed to the uppermost members of the group of mysticial vibrissae.

The labial division gives off a small branch which passes deeply and medially to supply the hairy skin of the most anterior part of the upper lip, together with the philtrum. The remainder of the nerve divides into some six branches. These are distributed to the several rows of vibrissae, a minute filament being given to each hair follicle. One or two twigs from the most lateral of these branches are fasciculated with filaments of the facial nerve.

Variation : In both specimens of the common shrew, the superior nasal branch was relatively bigger than in the two elephant shrews and supplied more filaments to the uppermost mysticial vibrissae. Although in three of the specimens it was not possible to trace any filaments of the nasal division as far as the philtrum, in the single available specimen of the four-toed elephant shrew, a clearly-defined filament of the inferior branch of the nasal division joined the philtral branch of the labial division and was distributed to the downwardly-projecting part of the rhinarium.

Relative to the branches supplying the skin of the upper lip and philtrum, those distributed to the mysticial vibrassae were considerably smaller in both species of elephant shrew than in either of the available specimens of the common shrew.

Order : LAGOMORPHA

Oryctolagus cuniculus—the rabbit (six specimens)

Order : RODENTIA (Fig. 1)

Sciurus sp.—the squirrel (two specimens)
Cricetus cricetus—the golden hamster (six specimens)
Rattus sp.—the rat (six specimens)
Mus sp.—the mouse (ten specimens)
Myocastor coypus—the coypu (one specimen)
Dasyprocta aguti—the agouti (one specimen)

The general arrangement of the maxillary nerve was sufficiently similar in all available representatives of the orders Lagomorpha and Rodentia to warrant their being considered together.

Facial features

The rhinarium is, in most species, relatively small, but in the coypu and agouti it is supplemented by a thickened folding of the skin of the medial side of the nares (Osman Hill, 1948). In all groups, a small, downwardly projecting process of the rhinarium lies deeply in the groove between the medial ends of the maxillary processes. Mysticial vibrissae are always well developed and form two clearly-defined bundles—an upper group on the side of the snout comprising shorter hairs than a lower group attached to the upper lip.

Maxillary nerve

In the available specimens, no variations were found in the mode of exit of the maxillary nerve from the skull, in the zygomatic and lacrimal nerves, or in the pattern of origin of the dental nerves.

Exit from cranium

The maxillary nerve, ensheathed in connective tissue, leaves the cranium through the infero-medial part of the orbital fissure. The ophthalmic division, surrounded by its own connective tissue sheath, passes through the supero-lateral part of this opening.

Zygomatic and lacrimal nerves

The zygomatic nerve takes origin within the cranial cavity from the maxillary division, but passes through the orbital fissure in the same connective tissue sheath as the ophthalmic division. It is extremely fine, and while passing laterally across the orbital floor gives a twig to the lacrimal branch of the ophthalmic division. It finally emerges on to the cheek to supply the small group of genal vibrissae and the adjacent skin.

Dental nerves

While lying on the orbital floor, the infraorbital nerve gives off a single posterior superior dental nerve. More anteriorly, several small middle and anterior superior dental nerves arise from its lateral side and pass into a series of canals leading towards the upper teeth.

Division of infraorbital nerve

General description : The infraorbital nerve splits into nasal and labial divisions immediately before entering the short infraorbital canal.

Variation : In the six specimens of the rabbit, in the two of the squirrel and in the six of the golden hamster, the nasal and labial divisions were approximately equal in size. In the dissections of rats and mice the labial division was slightly more prominent, but in the single specimens of the coypu and agouti the nasal division was much the bigger.

In two of the six specimens of the rabbit, a small accessory infraorbital foramen lay superior to the main opening. This transmitted a branch which

originated from the lateral (i.e. labial) side of the infraorbital trunk before its initial separation into nasal and labial divisions, and which, after emerging on to the face, passed downwards to supply the most posterior mysticial vibrissae. One or two of its twigs were fasciculated with those of the facial nerve.

Facial distribution

General description : After emerging from the infraorbital foramen, the nasal division of the infraorbital nerve gives off a superior branch which ramifies on the dorsum of the nose, giving twigs to the uppermost mysticial vibrissae and supplying the medial part of the rhinarium. The remainder of the division continues as the inferior branch which, lying deeply in the soft tissues of the face, passes forwards and downwards to supply the lateral part of the rhinarium together with the nasal vestibule.

The labial division of the infraorbital nerve divides repeatedly to form a leash of fibres that are distributed to the vibrissae and to the skin of the face and lip, their twigs extending as far as the median cleft between the maxillary processes. Two or three twigs from the most posterior branches of the labial division become fasciculated with those of the facial nerve.

Variation : In contrast to the other rodents and lagomorphs examined, the superior nasal branch was, in the coypu and agouti, bigger than the inferior branch, the additional fibres being distributed to the infolding of the medial part of the rhinarium.

Order : CARNIVORA (Fig. 2)

Canis familiaris—the dog (eleven specimens)
Mustela putorius—the ferret (nine specimens)
Lutra lutra—the otter (one specimen)
Felis catus—the cat (two specimens)
Phoca vitulina—the seal (one specimen)

Facial features

A rhinarium is present in all cases but varies in size. In the dog and cat, it is relatively big and a band of moist naked skin projects downwards to form the philtrum. In the ferret, the two halves of the upper lip are separated only by a sagittal groove, while in the otter and seal, not only is the rhinarium small and confined to the immediate surroundings of the nostrils, but the upper lip is undivided by even a shallow groove. Variable numbers of mysticial vibrissae are present, and although in some cases these extend on to the sides of the nasal cavity, they are not, as in many rodents, clearly separated into upper and lower bundles. Vibrissae are least numerous in the dog. In the cat, they are bigger and more numerous, whilst in the ferret, in addition to long thick vibrissae originating from the upper lip, there are strong hairs on the sides of the snout. In the otter, although only some twenty mysticial vibrissae are present bilaterally, each is much thicker than in the dog, cat or ferret. In this species the vibrissae on the sides of the snout are

quite as big as those on the upper lip. In the seal, the number of mysticial vibrissae is increased to forty, the lower members of the group being exceptionally well-developed and presenting a peculiarly twisted appearance. In this species, each follicle is up to 1·0 cm. long and is some 0·4 cm. in diameter.

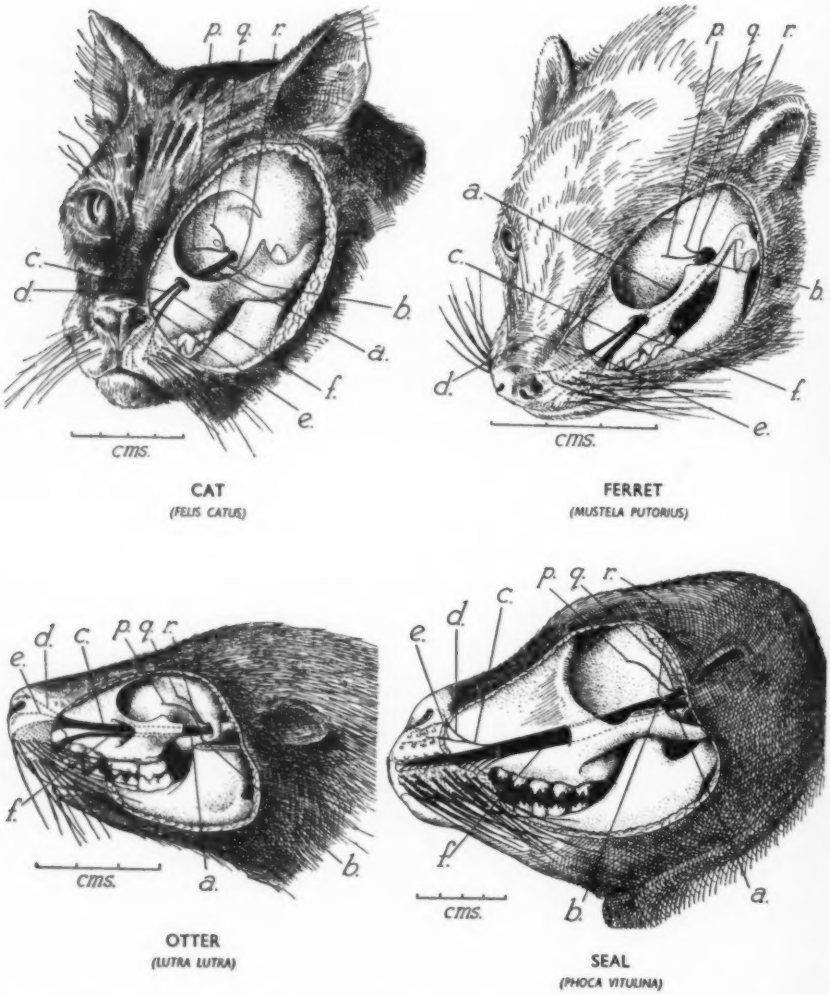


Fig. 2.—Variation in the maxillary nerve of certain carnivores. (*a*) Infraorbital nerve. (*b*) Zygomatic nerve. (*c*) Nasal division of infraorbital nerve. (*d*) Superior branch of nasal division of infraorbital nerve. (*e*) Inferior branch of nasal division of infraorbital nerve. (*f*) Labial division of infraorbital nerve. (*p*) Nasociliary branch of ophthalmic division of trigeminal nerve. (*q*) Frontal branch of ophthalmic division of trigeminal nerve. (*r*) Lacrimal branch of maxillary division of trigeminal nerve.

Maxillary nerve

Exit from cranium

General description : The maxillary and ophthalmic divisions emerge from the trigeminal ganglion and enter the orbit separately, the maxillary being lateral to the ophthalmic.

Variation : In all nine ferret specimens, and in the single specimen of the seal, the maxillary nerve, together with the branches of the ophthalmic division entered the orbit through a single orbital fissure. The two were however, separated by a fibrous band. In the single specimen of the otter, the maxillary and ophthalmic divisions were separated by a horizontal spicule of bone which partly divided the foramen, while in the specimens of the dog and cat the maxillary division passed through a distinct foramen rotundum, and the ophthalmic division through the superior orbital fissure.

Zygomatic and lacrimal nerves

General description: Both the zygomatic and lacrimal nerves are given off from the maxillary trunk as it emerges from the trigeminal ganglion. All three then pass through either the foramen rotundum or through the infero-lateral compartment of the orbital fissure. The zygomatic and lacrimal nerves do not, as in other mammalian orders, exchange filaments, but run parallel to each other through the periorbital fascia to end by supplying areas of skin around the outer canthus. The zygomatic branch also supplies the genal vibrissae. The ophthalmic division of the trigeminal nerve splits into frontal and nasociliary nerves only.

Variation

In all eleven available dogs, the zygomatic and lacrimal nerves arose separately from the main trunk. In the cat, ferret, otter and seal, however, they had a common origin, but separated before entering the orbit.

In the single available specimen of the otter, the zygomatic nerve was bigger than in the other forms and supplied the relatively big bundle of genal vibrissae.

Dental nerves

General description: The posterior superior dental nerves arise after the basic separation of the infraorbital nerve into nasal and labial divisions, but before these enter the infraorbital canal. The anterior superior dental nerves arise from the labial division while in the infraorbital canal.

Variation: No variations in the pattern of origin of the dental nerves were noted in any of the dissections in this group.

Division of infraorbital nerve

General description: The infraorbital nerve splits into nasal and labial divisions while lying on the orbital floor and before entering the infraorbital canal.

Variation: In the dog and cat (thirteen specimens) the nasal and labial divisions were of approximately equal size. In the single available otter,

the nasal division was much the bigger, while in the seal the labial division was grossly enlarged, this branch containing the majority of fibres of the maxillary trunk.

In the nine dissections of the ferret the labial division was somewhat bigger than the nasal, and in three of these specimens, the infraorbital canal was partly divided by a prominent bony ridge projecting upwards from its floor. The more medial compartment transmitted the nasal division and the more lateral the labial. In one specimen, the nasal division split while within the infraorbital canal, the deeply placed inferior branch running in a separate bony canal which opened on the surface of the maxilla, infero-medial to the main infraorbital foramen. In another of this series, branches of the labial division passing to the more anterior members of the group of mysticial vibrissae were encased in their own bony canal, whose aperture lay below and in front of the main infraorbital foramen.

Facial distribution

General description: The nasal division splits into superior and inferior branches, most fibres of the former terminating in the medial part of the rhinarium after a few filaments have been given off to the uppermost mysticial vibrissae. The inferior nasal branch is slightly the bigger and passes deeply to supply the lateral part of the rhinarium together with the medial and lateral walls of the nasal vestibule.

The labial division splits into a big branch which subdivides to supply the mysticial vibrissae, and a small twig which supplies the hairy skin of the medial part of the upper lip. A few twigs from the branches to the most posterior mysticial vibrissae are fasciculated with fibres derived from the facial nerve.

Variation: In all dissections of the dog and cat, a small twig of the inferior branch of the nasal division passed superficially to supply the downwardly projecting part of the rhinarium. In the other species, the nerve supply to the upper lip appeared to be derived entirely from branches of the labial division.

In the single available otter, the nasal division was very much bigger than the labial and before dividing into superior and inferior branches supplied twigs to the majority of the mysticial vibrissae. The reduced rhinarium was supplied by only a few twigs from the superior branch together with those from the inferior one.

In the single dissection of the seal both branches of the nasal division were exceptionally small. Before, however, sending twigs to the rhinarium, each supplied filaments to the eight uppermost vibrissae, these being the smallest of the mysticial group. A well-developed branch of the enormous labial division, some one or two mm. in diameter ramified around the base of each of the remaining vibrissae. A few fine filaments from this division also passed to the inside of the lip.

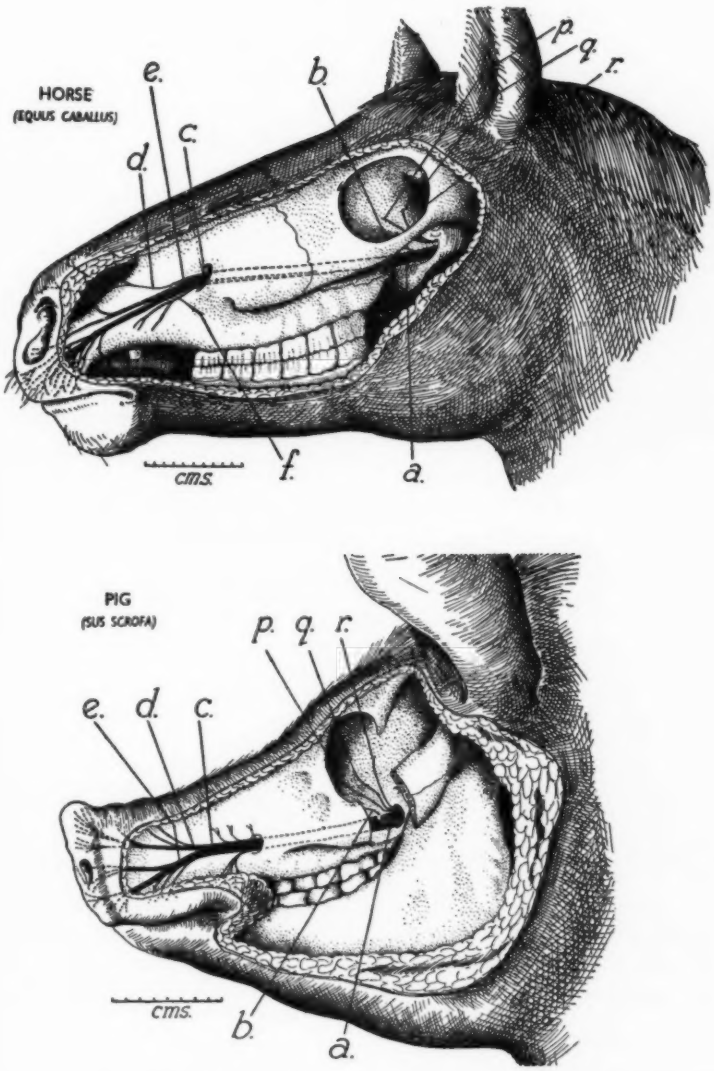


Fig. 3.—The maxillary nerve of the horse and pig. (*a*) Infraorbital nerve. (*b*) Zygomatic nerve. (*c*) Nasal division of infraorbital nerve. (*d*) Superior branch of nasal division of infraorbital nerve. (*e*) Inferior branch of nasal division of infraorbital nerve. (*f*) Labial division of infraorbital nerve. (*p*) Nasociliary branch of ophthalmic division of trigeminal nerve. (*q*) Frontal branch of ophthalmic division of trigeminal nerve. (*r*) Lacrimal branch of ophthalmic division of trigeminal nerve.

Order : PERISSODACTYLA (Fig. 3)

Equus caballus—the horse (four specimens)

Order : ARTIODACTYLA (Fig. 3)

Sus scrofa—the pig (ten specimens)
Bos taurus—the cow (seven specimens)
Ovis aries—the sheep (two specimens)

The main features of the maxillary nerve were sufficiently similar throughout this series to warrant the available members of the orders Artiodactyla and Perissodactyla being considered together.

Facial features

In the cow and sheep, the rhinarium is well developed and is covered with a complex series of dermal ridges. Its internarial part is wide, a broad process extending downwards to form a philtrum which completely separates the hairy parts of the upper lip.

In the horse, there is no moist naked rhinarium, but a diverticulum extends upwards from the nasal vestibule. The upper lip is covered completely with hairy skin and is undivided by even a sagittal groove.

In the pig, the rhinarium is replaced by a disc-like structure. The nares are set towards the centre of its anterior surface, and, as in the horse, cow and sheep, the upper lip is undivided.

The upper lip of ungulates is mobile, being but loosely attached to the anterior margin of the gum. Vibrissae are, in the four types considered in this section, greatly reduced, being frequently represented by mere sinus hairs.

Maxillary nerve

Exit from cranium

General description: The maxillary and ophthalmic divisions of the trigeminal nerve leave the cranial cavity through the orbital fissure, each being surrounded by its own sheath of connective tissue and the maxillary division lying lateral to the ophthalmic. The maxillary division then passes forwards on the orbital floor.

Variation: In each of the four specimens of the horse, but not in any of the nineteen dissections of pig, sheep or cow, the orbital fissure was partly divided by a horizontal shelf of bone into superior and inferior compartments. The first transmitted the ophthalmic division, the second, the maxillary.

Zygomatic and lacrimal nerves

General description: The zygomatic nerve arises from the maxillary trunk, and passes laterally through the periorbital fascia to supply an area of skin near the outer canthus. A fine filament connects the zygomatic and lacrimal nerves.

Variation: In one specimen of the cow and in one of the pig, the zygomatic nerve separated from the maxillary trunk in the sphenopalatine fossa, subsequently passing into the periorbital fascia through a spiral opening. In

all other instances, the zygomatic branch separated from the main trunk after it had entered the orbit. In three specimens of the pig the zygomatic nerve was divided into two distinct filaments, while in a further two dissections of this species it was split into three filaments.

Dental nerves

General description: After entering the orbit, the infraorbital nerve gives off two or three posterior superior dental filaments which pass into fine canals in the maxillary tuberosity. More anteriorly, the labial division gives off a number of fine middle superior dental nerves.

Variation: An anterior superior dental nerve was not found in any of the dissections of cow or sheep, these animals lacking upper incisor teeth. However, the most anterior of the middle superior dental filaments was, in these cases, relatively big. In all available specimens of the horse and pig, an anterior superior dental nerve passed laterally into a bony canal in the maxilla to supply the anterior teeth.

In nine of the ten dissections of the pig, the middle and anterior superior dental nerves arose from the lateral side of the undivided infraorbital nerve as it traversed the infraorbital canal. In the tenth specimen, these branches arose from the labial division.

Division of infraorbital nerve

General description: The infraorbital nerve splits into nasal and labial divisions while passing through the exceptionally long infraorbital canal. The nasal division is very much bigger than the labial.

Variation: In contrast to the condition seen in the sheep (two dissections) in the horse (four dissections) and in a single dissection of the pig, the small labial division in each of the four available specimens of the cow emerged through an accessory infraorbital foramen lying infero-lateral to the main opening.

In nine of the ten specimens of the pig there was no primary subdivision of the infraorbital nerve, the entire trunk apparently corresponding to the nasal division. In the tenth specimen, a labial division, very much smaller than the nasal, separated from the lateral side of the infraorbital nerve as this traversed the infraorbital canal.

Facial distribution

General description: The nasal division splits into a small superior and a bigger inferior nasal branch. The former ramifies on the dorsum of the snout, some of its twigs reaching the extreme anterior end. The inferior nasal branch divides into superficial and deep bundles. The superficial bundle gives twigs to the anterior region of the upper lip even in those forms (horse and pig) where there is no downwardly projecting part to the rhinarium. The deep bundle is distributed to the nasal vestibule.

After emerging on to the face, the labial division splits into two small branches which supply an area of skin on the posterior part of the upper lip near the corner of the mouth. They receive one or two fine filaments from the facial nerve.

Variation: In the dissections of the cow and sheep, the terminal twigs of the superior nasal branch supplied the upper and medial parts of the rhinarium. The inferior nasal branch of these forms was distributed superficially to the downwardly-projecting process of the rhinarium together with the adjacent part of the upper lip, and deeply to the vestibule of the nose and the lateral part of the rhinarium.

In all four dissections of the horse the superior branch of the nasal division was finer than in the available specimens of the cow and sheep. In these three species the superficial bundle from the inferior branch was, however, exceptionally big, sending numerous branches to areas of both the inner and outer surfaces of the upper lip, extending from the corners of the mouth to the mid-line. Most fibres of the deeper bundle of the inferior branch of the nasal nerve were distributed to the nasal vestibule, but in each of the dissections of the horse one distinct filament passed to the nasal diverticulum.

In all ten dissections of the pig the most anterior twigs of the superior nasal branch supplied both the rim and the upper part of the anterior surface of the disc-like ending of the snout, the remainder ramifying on the surface of the snout. In this series, in addition to supplying the upper lip, some twigs of the superficial bundle of the inferior nasal branch were distributed to the area of skin between the snout and upper lip, and to the lower part of the rim of the disc-like ending of the snout. In the nine specimens wanting any labial division a few filaments of the superficial bundle of the inferior nasal branch passed posteriorly to supply the skin behind the angle of the mouth. In all ten dissections, the deep bundle of the inferior nasal branch divided into three : one group of fibres supplied the inferior part of the surface of the disc, another its internarial part, while a third was distributed to the area of the snout lateral to the nares, some of its fibres reaching the vestibule of the nose.

DISCUSSION

The present study, although in many ways less complete than could be desired, has shown that the basic pattern of branching of the maxillary nerve already established for the Primates (Ashton & Oxnard, 1958), is characteristic of a number of other orders of placental mammals. Certain variations have emerged, and whereas some have no obvious adaptive significance, others can, as in Primates, be readily correlated with variations in facial features.

In the first group of variations, the most obvious concerns the mode of origin of the lacrimal nerve which, in most mammalian orders, derives from the ophthalmic division and is connected to the zygomatic branch by a filament of nervous tissue. In carnivores, however, the lacrimal nerve is a branch of the maxillary trunk, and in this order, the zygomatic and lacrimal nerves are not mutually connected. This difference is apparently unrelated to any noteworthy variations in either the lacrimal gland or the cutaneous distribution of the zygomatic and lacrimal nerves. It appears to be equally unrelated to the relative disposition of the maxillary and ophthalmic trunks, for although in contrast to many mammalian orders, the maxillary trunk of carnivores lies lateral to the ophthalmic division (Lacroix, 1927), a similar

arrangement in insectivores and ungulates is not associated with any peculiarities of origin of the lacrimal nerve.

The second major group of variations in the maxillary nerve—i.e. those which can be readily correlated with variations in facial structure—affect chiefly the proportions of the nasal and labial divisions of the infraorbital nerve. The differences of this type that have emerged from the present study have not only reinforced the earlier conclusion (Ashton & Oxnard, 1958) that an increase in the size of the nasal division is associated with the development of a rhinarium, but have also made it clear that the proportions of the nasal and labial divisions are affected by the development of mysticial vibrissae. If the inferior members of the group of mysticial vibrissae are enlarged (cf. for example, the ferret and cat), the size of the labial divison of the infraorbital nerve is correspondingly increased. Conversely in those isolated cases (e.g. the otter) where the superior members of the group—i.e. those which in non-primate mammals generally receive twigs from the nasal division—are relatively big, the nasal division is increased in size. The contrast between these two groups is most striking if the condition in the otter is compared with that in the seal—an animal in many ways similar in facial structure but in which it is the lower members of the group of mysticial vibrissae that are highly developed and whose labial division is correspondingly big.

The present analysis has also confirmed the opinion that a number of additional facial features can affect the distribution of the infraorbital nerve. Of these, one of the most spectacular occurs in the pig where the vast majority of fibres of the infraorbital nerve are distributed to the disc-like ending of the snout.

In addition to their application to these purely taxonomic questions, the data summarized in the present paper bear strongly on the suggestion advanced in our earlier study (Ashton & Oxnard, 1958), that the nasal division of the infraorbital nerve supplies structures derived from the embryonic frontonasal process, while the labial division supplies those derived from the maxillary processes. Thus, the downwardly projecting part of the rhinarium when present is presumably a derivative of the embryonic frontonasal process (Boyd, 1932) and in a number of cases (e.g. dog, cat) it has been established that filaments of the nasal division penetrate into this region. Again, the hairy lateral parts of the upper lips are almost certainly derivatives of the maxillary processes and are, in the majority of cases (e.g. carnivores, rodents, insectivores) supplied by branches of the labial division. To this rule, however, the ungulates appear to be a noteworthy exception, for the mobile upper lip is, in this group, supplied by a relatively big bundle of fibres arising from the inferior branch of the nasal division.

ACKNOWLEDGMENTS

Our best thanks are due to Professor Sir Solly Zuckerman, C.B., F.R.S., for suggesting this study to us and for his continued interest in the work, to Professor A. J. E. Cave for some useful criticism, and to Mr W. J. Pardoe to

whom we owe the text figures. Part of the material was supplied by the Zoological Society of London.

SUMMARY

1. A study has been made of the maxillary nerve in eighty-three specimens of nineteen species of placental mammals. The series included representatives of six mammalian orders.

2. In this material, the maxillary trunk first gives off the zygomatic nerve and then passes forwards on the orbital floor. It gives origin to the posterior and anterior superior dental nerves, and splits at a variable point into nasal and labial divisions. The nasal division supplies the surface of the snout, the rhinarium and the vestibule of the nose, frequently giving twigs to the uppermost members of the group of mysticial vibrissae. The labial division is distributed to the remainder of the mysticial vibrissae, and to the skin of the cheek and upper lip.

3. If the rhinarium or the uppermost mysticial vibrissae are prominent, the nasal division is correspondingly big.

4. If the lower members of the group of mysticial vibrissae are well developed, it is the labial division that is relatively enlarged.

5. The relative sizes of the facial branches of the infraorbital nerve are also affected by the development of specialized facial features—e.g. in the pig the vast majority of nerve fibres are distributed to the disc-like ending of the snout.

6. Certain structures presumably derived from the frontonasal process receive their nerve supply from the nasal division, while those derived from the maxillary processes are normally supplied by fibres from the labial division. In the ungulates, however, the nerve supply to the mobile upper lip is derived from branches of the nasal division.

REFERENCES

Ashton, E. H. & Oxnard, C. E. (1958). Some variations in the maxillary nerve of Primates. *Proc. zool. Soc. Lond.* **131,** 457.

Boyd, J. D. (1932). The classification of the upper lip in mammals. *J. Anat., Lond.* **67,** 409.

Bradley, O. C. (1927). *Topographical anatomy of the dog.* (Second edition) London and Edinburgh : Oliver and Boyd.

Ellenberger, W. & Baum, H. (1894). *Anatomie descriptive et topographique du chien.* Paris : Reinwald.

Hill, W. C. Osman (1948). Rhinoglyphics : epithelial sculpture of the mammalian rhinarium. *Proc. zool. Soc. Lond.* **118,** 1.

Hines, M. (1929). The brain of *Ornithorhynchus anatinus*. *Phil. Trans.* (B) **217,** 155.

Huber, E. (1930). Evolution of facial musculature and cutaneous field of trigeminus. *Quart. Rev. Biol.* **5,** 133 & 389.

Lacroix, M. R. (1926). Considérations sur les rapports des nerfs lacrymal et orbitaire chez les mammifères supérieurs et chez l'homme. *Arch. Anat., Strasbourg* **6,** 33.

Pocock, R. I. (1914). On the facial vibrissae of Mammalia. *Proc. zool. Soc. Lond.* **1914,** 889.

Schulte, H. von W. & Forest Smith, M. de (1918). The external characters, skeletal muscles and peripheral nerves of *Kogia breviceps* (Blainville). *Bull. Amer. Mus. nat. Hist.* **38,** 7.

Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* **85,** 1.

SISSON, S. (1930). *The anatomy of the domestic animals.* (Second edition) Philadelphia and London : Saunders.

SONNTAG, C. F. & WOOLLARD, H. H. (1925). A monograph of *Orycteropus afer–11* Nervous system, sense-organs and hairs. *Proc. zool. Soc. Lond.* **1925,** 1185.

STUBBS, G. (1776). *The anatomy of the horse.* London : Heywood Hill. (Reprinted 1938.)

WINCKLER, G. (1932). Les nerfs de l'orbite et le ganglion ophtalmique dans la série des mammifères et chez l'homme. *Arch. Anat., Strasbourg* **14,** 301.

ON A COLLECTION OF LANCELETS FROM THE GAMBIA, WITH A DESCRIPTION OF A NEW SPECIES OF *BRANCHIOSTOMA*

BY

J. E. WEBB

Department of Zoology, University College, Ibadan

[Accepted 15th April 1958]

(With 2 figures in the text)

CONTENTS

	Page
Introduction	627
Systematic account	628
Branchiostoma senegalense Webb	628
Branchiostoma leonense Webb	628
Branchiostoma gambiense sp. n.	628
A comparison of *B. gambiense* with other West African lancelets	629
Conclusions	633
References	635

INTRODUCTION

The lancelets of West Africa include *Branchiostoma senegalense* from the coasts of Rio de Oro and the Senegal and a series of Guinea Coast species, *B. leonense*, *B. takoradii*, *B. nigeriense* and *B. africae*, from localities between Sierra Leone and the Cameroons (see Webb, 1955 and 1956). *B. senegalense* occurs in the cold waters of the North-South Canaries Current while the Guinea Coast lancelets are in the warm waters of the West-East Guinea Current. The Guinea Coast lancelets have been shown to be most nearly related to the Cape lancelet, *B. capense* (see Webb, 1957), while the more northerly *B. senegalense* appears to have somewhat tenuous affinities with both the Guinea Coast group and the English Channel population of *B. lanceolatum* (see Webb, 1956 a). The distribution of these lancelets, therefore, evidently follows the pattern of currents in the West African coastal waters. As the Canaries and Guinea currents meet off the Gambia, the lancelet fauna of this region is likely to be of particular interest for it is here that the distribution of *B. senegalense* and *B. leonense*, the most westerly of the Guinea Coast species, may overlap and opportunities for hybridization occur. If *B. senegalense* and *B. leonense* can be shown to be sympatric over part of their range at least, then the validity of these species can be considered established.

In December, 1956, the research vessel "Cape St. Mary" of the West African Fisheries Research Institute visited the Gambia, and Mr Alan Longhurst collected lancelets from six localities in this area. This paper is a report on his collection. Details of the bottom deposits and the temperature and salinity of the water at the stations where lancelets were taken are given by Mr Longhurst (1958) in a paper on the ecology of this region.

The author is grateful to Mr Longhurst for permission to describe his collection of lancelets.

SYSTEMATIC ACCOUNT

Family BRANCHIOSTOMIDAE

BRANCHIOSTOMA SENEGALENSE Webb

Branchiostoma africae (nec Hubbs in Monod), in Poll (1949).
Branchiostoma senegalense Webb (1955, 1956, 1956 a).

Localities.—" Cape St. Mary " Station MB6/A1, 13° 30′ N., 16° 54′ 30″ W. one specimen 7 mm. (B.M. reg. no. 1958.3.28.1) taken in 16 metres of water from shelly sand ; Station MB6/A2, 13° 30′ N., 17° 06′ W. one specimen 8 mm. (B.M. reg. no. 1958.3.28.2) taken in 29 metres of water from shelly sand ; Station MB6/B6, 13° 21′ N., 17° 05′ W. one specimen 8 mm. (B.M. reg. no. 1958.3.28.5) taken in 28 metres of water from shelly sand. The specimens from each locality were taken with a 0·1 m.² Smith sampler in five consecutive hauls as close together as possible on 23rd, 24th and 26th December, 1956.

Remarks.—These specimens agree with the diagnosis for *B. senegalense* published by Webb (1955) and based on specimens from the Island of Gorée near Dakar. The distribution of this species may be presumed to extend along the West African coast at least from latitude 13° 30′ N. to latitude 24° N.

BRANCHIOSTOMA LEONENSE Webb.

Branchiostoma leonense Webb (1956, 1956 a, 1957).

Localities.—" Cape St. Mary " Station MB6/B5, 13° 22′ N., 17° 08′ W. one specimen 18 mm. (B.M. reg. no. 1958.3.28.3) taken in 48 metres of water from shelly sand ; station MB6/B6, 13° 21′ N., 17° 05′ W. one specimen 24 mm. (B.M. reg. no. 1958.3.28.4) taken in 28 metres of water from shelly sand ; Station MB6/C1, 13° 34′ 30″ N., 16° 43′ W. five specimens 14–28 mm. (B.M. reg. nos. 1958.3.28.6–7) taken in 8 metres of water from shelly sand. The specimens from each locality were taken with a 0·1 m.² Smith sampler in five consecutive hauls as close together as possible on 25th, 26th and 27th December, 1956.

Remarks.—These specimens agree with the diagnosis for *B. leonense* published by Webb (1956) and based on a series of specimens from the Sierra Leone River Estuary. The distribution of this species, therefore, may be presumed to extend along the West African coast at least from latitude 8° 36′ N. to 13° 34′ N.

BRANCHIOSTOMA GAMBIENSE sp. n.

Type specimens.—Holotype (B.M. reg. no. 1958.3.28.15) 29 mm. ; no gonads are present. This specimen has been preserved in 70 per cent alcohol. Paratypes comprise sixteen specimens preserved in 70 per cent alcohol (B.M. reg. nos. 1958.3.28.11–14) ranging in length from 27–32 mm. Ten of the paratypes possess small or very small gonads and include both the largest and

the smallest specimens in the series. The holotype and the paratypes are deposited in the British Museum (Natural History).

Other material.—The collection included six other specimens more or less damaged or distorted. These are preserved in 70 per cent alcohol and are retained in the British Museum, reg. nos. 1958.3.28.8–10.

Type locality.—" Cape St. Mary " Station MB6/D1, off the Gambian coast 13° 10′ N., 16° 59′ W. Specimens were taken with a 0·1 m.² Smith sampler in five consecutive hauls as close together as possible in 18 metres of water from shelly sand on 28th December 1956.

Diagnosis.—In the following diagnosis counts and measurements have been made on seventeen specimens and examined statistically.

1. Dorsal fin chambers number 318–394 : Mean 362 : Standard Deviation 18·47 : S.D.=5·1 per cent of the Mean.

2. Preanal fin chambers number 39–56 : Mean 46·8 : Standard Deviation 5·5 : S.D.=11·8 per cent of the Mean.

3. Tallest of dorsal fin chambers 2·0–3·3 times as high as broad : Mean 2·7 : Standard Deviation 0·36 : S.D.=13·2 per cent of the Mean.

4. Height of dorsal fin contained 9–14 times in the depth of the body in the mid-atrial region : Mean 11·5 : Standard Deviation 1·42 : S.D.=12·3 per cent of the Mean.

5. Postatrioporal region 0·30–0·37 the length of the preatrioporal region : Mean 0·343 : Standard Deviation 0·022 : S.D.=6·4 per cent of the Mean.

6. Myotomes from anterior end to atriopore 43–46 : Mean 45·3 : Standard Deviation 0·94 : S.D.=2·1 per cent of the Mean.

7. Myotomes from atriopore to anus 12–15 : Mean 13·9 : Standard Deviation 0·71 : S.D.=5·1 per cent of the Mean.

8. Myotomes posterior to anus 11–12 : Mean 11·8 : Standard Deviation 0·44 : S.D.=3·7 per cent of the Mean.

9. Total myotomes 68–72 : Mean 70·4 : Standard Deviation 1·12 : S.D.= 1·6 per cent of the Mean.

10. Maximum length in sample examined 33 mm. ; minimum length 27 mm.

The following characters not suitable for numerical evaluation assist in the recognition of this species and are illustrated in Fig. 1, which has been prepared from *camera lucida* drawings of the holotype. The rostrum is comparatively short and tends to be slightly upturned at the tip giving rise to a shallow post-rostral notch of varying prominence. The dorsal fin is slightly higher anteriorly and posteriorly than in the centre. The caudal fin is comparatively small and is not indented in outline either dorsally or ventrally in the subterminal region. The caudal fin merges almost imperceptibly into the preanal fin which is relatively broad with fin chambers extending little more than half the total breadth of the fin. The buccal cirri appear to be fringed with minute lateral projections or none at all.

A COMPARISON OF *B. gambiense* WITH OTHER WEST AFRICAN LANCELETS

As *B. gambiense* occurs in the same area as *B. leonense* and *B. senegalense*, it is desirable that a detailed comparison should be made between *B. gambiense*

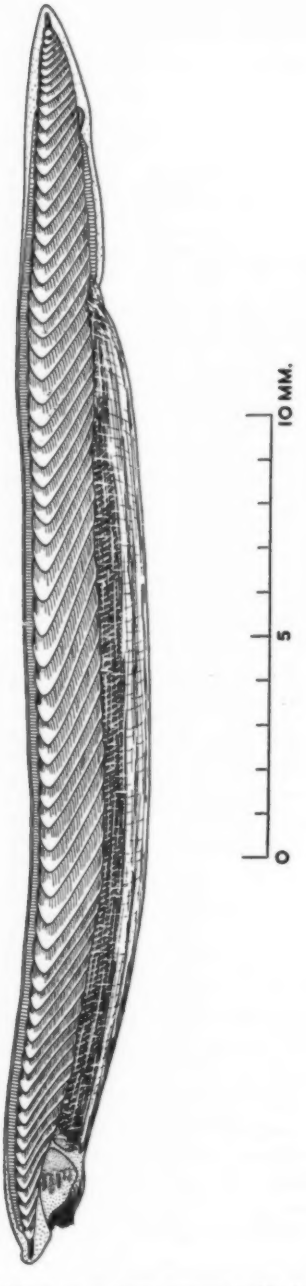


Fig. 1.—*Branchiostoma gambiense* sp. n. from *camera lucida* drawings of the holotype.

and these two species. In Table 1, the Means, the Standard Deviations and the Standard Deviations as a percentage of the Mean of the nine characters numerically evaluated in the diagnoses for the three species are compared, and "*t*" and hence "P" is calculated to show the extent of the differences between the samples. In the comparison between *B. gambiense* and *B. leonense*, the value of "*t*" for all characters numbered from 1–8 in the diagnosis is very high and "P" accordingly is less than 0·001, while even in character 9 (the total number of myotomes) the difference is significant since "P" is less than the value 0·05 taken to be the limit of significance. It is clear, therefore, from this analysis that *B. gambiense* and *B. leonense* must be regarded as distinct. In support of this it is noted that the form of both the rostrum and the caudal fin is different in the two species.

Similarly the comparison between *B. gambiense* and *B. senegalense* in Table 1 indicates that the differences are highly significant in all diagnostic characters except the number of myotomes in the tail (character 8) and even here the value for "P" is less than 0·02. Moreover, the form of the rostrum and particularly of the caudal fin is different in the two species and thus supports the view that *B. gambiense* and *B. senegalense* are distinct.

It remains to compare *B. gambiense* with the other lancelets of the Guinea Coast group *B. leonense*, *B. takoradii*, *B. nigeriense* and *B. africae* (Webb, 1956 and 1956 a). *B. gambiense* is similar to these forms in the high number of dorsal fin ray chambers present, the low postatrioporal ratio, in the number of myotomes in the tail and in the total myotome number (characters 1, 5, 8 and 9), although the actual values for these characters in all these species are different in every case (see Webb, 1955, 1956 and 1956 a). With regard to the remaining characters, in *B. gambiense* the number of preanal fin chambers (character 2) is considerably lower than in any other lancelet in the group, the height of the dorsal fin is also less (see characters 3 and 4) and there is an increase in the number of anterior myotomes at the expense of the number between the atriopore and the anus (see characters 6 and 7) which is not found in the other species with the possible exception of *B. africae*. It does not appear that this new Gambian lancelet can be considered as an aberrant form of any of the more easterly species and it must, therefore, be presumed that three distinct lancelets occur in the Gambian waters.

Webb (1956 a) compared the diagnostic characters of the West African lancelets with those of various populations of *B. lanceolatum* from European waters and demonstrated the existence of certain trends in their Mean values. When *B. gambiense* is considered in relation to this series it is found that none of the mean values for that species, with the exception of the figure for the number of dorsal fin chambers (character 1), is intermediate between the corresponding values for the species *B. senegalense* and *B. leonense* which occur geographically on either side of it. Moreover, where the mean values for *B. gambiense* can be included in a trend, it is always with an existing trend in the Guinea Coast group and not in the *lanceolatum-sengalense* series. This evidence suggests that the affinities of *B. gambiense* lie with the Guinea Coast lancelets.

TABLE 1

A statistical analysis showing to what extent the differences between samples of *B. gambiense*, *B. leonense* and *B. sengalense* may be held to characterize the populations from which samples were taken.

Character No.	*B. gambiense*			*B. leonense*			"*t*"	"P"	*B. senegalense*			"*t*"	"P"
	Mean	S.D.	S.D. as % of Mean	Mean	S.D.	S.D. as % of Mean			Mean	S.D.	S.D. as % of Mean		
1	362	18·47	5·1%	382	15·19	3·97%	3·74	<0·001	296	13·4	4·6%	12·2	<0·001
2	47	5·5	11·8%	58	3·15	5·44%	8·03	<0·001	51·5	3·2	6·2%	3·03	>0·002
3	2·7	0·36	13·2%	5·35	0·59	11·0%	16·2	<0·001	3·15	0·35	11·1%	3·74	0·001
4	11·5	1·42	12·3%	8·0	0·82	10·2%	9·9	<0·001	9·6	1·16	12·0%	4·36	<0·001
5	0·343	0·022	6·4%	0·380	0·021	5·53%	5·35	<0·001	0·5	0·023	4·6%	20·7	<0·001
6	45·3	0·94	2·1%	43·24	1·33	3·08%	5·4	<0·001	40·25	0·6	1·5%	19·1	<0·001
7	13·9	0·71	5·1%	15·52	0·59	3·78%	7·8	<0·001	17	0·63	3·7%	13·6	<0·001
8	11·8	0·44	3·7%	10·4	0·65	6·20%	7·5	<0·001	11·35	0·57	5·0%	2·57	<0·02
9	70·4	1·12	1·6%	69·16	1·92	2·78%	2·35	>0·02	68·6	0·86	1·3%	5·37	<0·001

CONCLUSIONS

The locations of the six sampling stations of the "Cape St. Mary" research cruise in Gambian waters at which lancelets were found are shown on the map in Fig. 2 together with an indication of the lancelet species taken at each. Three different lancelets were collected from the area. These were referable either to *B. senegalense* or to *B. leonense* or to the form here described as *B. gambiense*. In view of the fact that, in the comparatively limited area sampled, both *Branchiostoma leonense* and *B. senegalense* were taken and in one instance

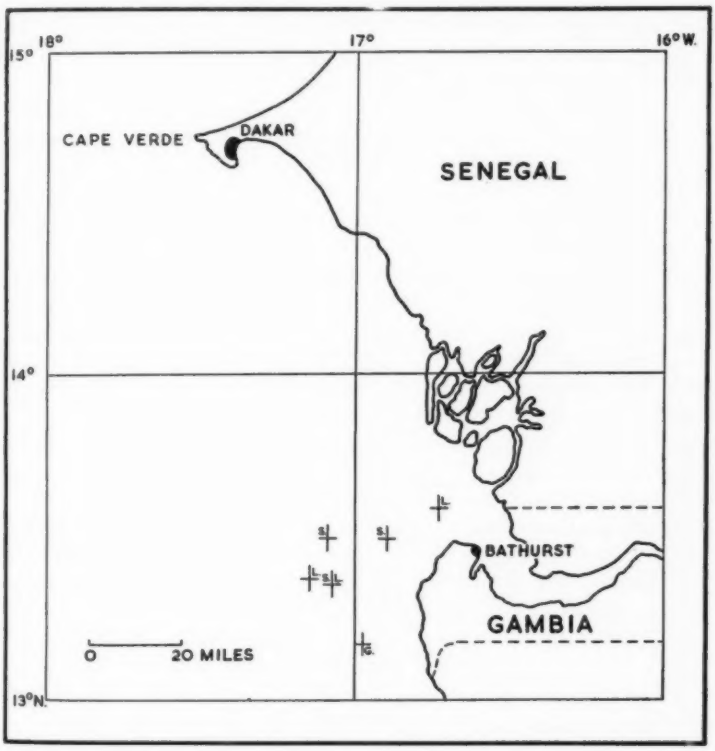


Fig. 2.—Map showing the stations at which lancelets taken were during the "Cape St. Mary" cruise to the Gambia. G = *B. gambiense*, L = *B. leonense*, S = *B. senegalense*.

at the same station, it is reasonable to assume that the range of these two species overlaps and that in this region they are sympatric. *B. leonense* is the most westerly of the lancelets of the Guinea Coast group and its distribution is thus now known to extend from the Gambia to Freetown in Sierra Leone, a distance of a little under 450 miles. *B. senegalense*, on the other hand, is the lancelet of the cold Canaries Current and its distribution is known to extend from Villa Cisneros in Rio de Oro to the Gambia, a distance of nearly 800 miles.

The occurrence of both these lancelets in the Gambian waters, therefore, raises the question of whether hybridization takes place.

It has been shown that *B. gambiense*, except in the number of dorsal fin ray chambers, is not intermediate in any of its diagnostic characters between *B. senegalense* and *B. leonense* and, moreover, the sample of seventeen specimens analysed shows a degree of variability of the same order as that of the Senegal and Sierra Leone lancelets (see Table 1). In addition, *B. gambiense* was taken at one locality only, no specimens referable to *B. senegalense* or *B. leonense* were present in that sample and no specimens of *B. gambiense* were taken at any of the localities where either or both of these two species were found. It does not seem probable, therefore, that *B. gambiense* is a hybrid of *B. senegalense* and *B. leonense* and for these reasons it has been described as a new species.

The presence of both *B. senegalense* and *B. leonense* in the waters off the Gambia where the Canaries and Guinea currents meet was not unexpected, but the occurrence of a third species in that area is remarkable. Webb & Hill (1958) have described the way in which adults of *B. nigeriense* congregate in suitable areas of sandy bottom prior to spawning and the nature of the deposits from which these three species from the Gambia were taken suggests that the behaviour of these lancelets, too, is similar to that of the Nigerian species. It is also probable that their larval life will not be greatly different in duration from that of *B. nigeriense* (see Webb, 1958) and that there would be ample time for dispersal to take place during the planktonic phase. Individuals of all three species, therefore, would be expected to be found congregating in all sand deposits of the appropriate grade (see Webb & Hill, 1958 and Webb, 1958a) unless the distribution of the larvae is limited by local water movements. Hybridization under such circumstances should take place if the forms are not incompatible and if the periods of spawning coincide. The specimens collected during the "Cape St. Mary" cruise, however, were not all of the same size. Those of *B. senegalense* were juvenile and did not exceed 8 mm. in length as compared with the maximum recorded length of 50 mm. for the adult of that species (see Webb, 1955). The specimens of *B. leonense*, on the other hand, ranged from 14–28 mm. and this species is known to reach maturity at a length of 28 mm. and to grow to a maximum length of 37 mm. (see Webb, 1956). These figures suggest that *B. senegalense* and *B. leonense* mature at different times and this may be the reason why hybrids were not found.

The specimens in the sample of *B. gambiense* ranged in length from 27–32 mm. and some of these were approaching maturity as small gonads were present. Their degree of development, therefore, was a little in advance of that of *B. leonense* from the same area. If, however, the spawning period of these two species is as prolonged as that in *B. nigeriense* (see Webb, 1958) and occupies about three months or more then it seems that some coincidence of spawning period in *B. gambiense* and *B. leonense* is likely to occur and failure of these species to hybridize must be due to other causes such as genetic incompatibility or isolation imposed by water movements.

This is not the first instance where different species of lancelet have been shown to be sympatric. *B. lanceolatum* was taken in the same haul as *B.*

arabiae in 1933 by the "John Murray" Expedition off the Arabian coast (Webb, 1956 b) and again with *B. belcheri* at Linga-linga in Portuguese East Africa (Webb, 1957), while at Singapore both *B. belcheri* and *B. malayana* (Webb, 1956 c) are known to occur. It is also probable that the Indian species *B. tattersalli*, *B. indicum* and *B. haekelii* are sympatric. There is reason to believe, therefore, that, in spite of the relatively close similarity of lancelets of the genus *Branchiostoma*, many if not all of the species are valid. It is important to establish this as the distribution of the different lancelet species appears to be so closely linked with water movements, often of a quite local character, that the lancelets may serve as valuable indicator organisms showing the extent of patches of water isolated by current movements. This is evidently so along the apparently relatively uniform West African coast where the occurrence of a series of different lancelets indicates the presence of previously unsuspected pockets of isolated water.

REFERENCES

Longhurst, A. R. (1958). An ecological survey of the West African marine benthos. *Fish. Publ. Colonial Office, Lond.* (in the press).

Poll, M. (1949). Résultats Scientifiques des Croisières du Navire—École Belge "Mercator", IV, *Mem. Inst. Sci. nat. Belg.* (2) no. **33,** 183.

Webb, J. E. (1955). On the lancelets of West Africa. *Proc. zool. Soc. Lond.* **125,** 421–443.

Webb, J. E. (1956). Cephalochordata of the coast of Tropical West Africa. *Atlantide Rep.* No. 4, 167–182.

Webb, J. E. (1956 a). On the populations of *Branchiostoma lanceolatum* and their relations with the West African lancelets. *Proc. zool. Soc. Lond.* **127,** 125–140.

Webb, J. E. (1956 b). Cephalochordata. *Sci. Rep. "John Murray" Exped.* **10,** 121–128.

Webb, J. E. (1956 c). A note on the lancelets of Singapore, with a description of a new species of *Branchiostoma*. *Proc. zool. Soc. Lond.* **127,** 119–123.

Webb, J. E. (1957). On the lancelets of South and East Africa. *Ann. S. Afr. Mus.* **43,** 249–270.

Webb, J. E. (1958). The ecology of Lagos Lagoon. Part III. The life-history of *Branchiostoma nigeriense* Webb. *Phil. Trans.* (B) **241,** 335–353.

Webb, J. E. (1958 a). The ecology of Lagos Lagoon. Part V—some physical properties of lagoon deposits. *Phil. Trans.* (B) **241,** 393–419.

Webb, J. E. & Hill, M. B. (1958). The ecology of Lagos Lagoon. Part IV—On the reactions of *Branchiostoma nigeriense* Webb to its environment. *Phil. Trans.* (B) **241,** 355–391.

SHELL FORM, PALLIAL ATTACHMENT AND THE LIGAMENT IN THE BIVALVIA

BY

GARETH OWEN

Department of Zoology, University of Glasgow

[Accepted 15th April 1958]

(With 6 figures in the text)

CONTENTS

	Page
Introduction	637
The adductor muscles	638
The ligament	643
Acknowledgments	647
Summary	647
References	648

INTRODUCTION

Primitively, the ligament in the Bivalvia comprises a superficial periostracum and outer and inner layers of the ligament. The inner layer is secreted by the epithelium of the mantle isthmus while the periostracum and outer layer are secreted by the inner and outer surfaces respectively of the outer marginal fold at the anterior and posterior ends of the ligament (Owen, Trueman & Yonge, 1953). Throughout the Bivalvia this primary ligament represents the basis of the ligament, but in most bivalves the outer folds of the mantle margins anterior and posterior to the mantle isthmus are fused, to a greater or less extent, resulting in some degree of secondary extension of the primary ligament (Yonge, 1957). Fusion of the inner periostracal-secreting surfaces of the outer folds results in extension by way of periostracum while where the outer surfaces of these folds are fused, extension of the primary ligament is by way of fusion layer and the result is the formation of a fourth layer in the ligament. Yonge (1957) has suggested that "each natural group of the Lamellibranchia has a characteristic pattern of mantle fusion involving the ventral margins, the siphons and the ligament". It is, therefore, of some importance to distinguish between secondary extension of the primary ligament by periostracum (secreted by the fused *inner* surfaces of the outer folds) on the one hand, and secondary extension by fusion layer on the other (secreted by the fused *outer* surfaces of the outer folds). Periostracum and fusion layer are frequently similar in appearance and, moreover, although it is usually possible to determine from sections the extent of fusion of the outer mantle folds, the colour reactions of periostracum and of fusion layer with type stains show considerable variation (Beedham, 1958).

From an examination of the structure of the ligament of a variety of bivalves it was noted that the extent of pallial attachment in the fused dorsal regions of the mantle margins, and hence of the pallial line on the internal

surface of the shell, was associated with the degree of fusion of the outer folds of the mantle margins anterior and posterior to the mantle isthmus. In this paper it is suggested that the type of secondary extension of the ligament (i.e. periostracum or fusion layer) can be readily determined in most bivalves from the disposition of the pallial line on the internal surface of the valves.

The probable course of evolution of the Bivalvia from ancestors possessing a simple dome-like shell has been outlined by Yonge (1947, 1953 a). In the Bivalvia the mantle is greatly extended, laterally compressed, and partially divided into two lobes connected dorsally by the mantle isthmus, the shell in this region being largely uncalcified and constituting the ligament (Owen, Trueman & Yonge, 1953). Early in the evolutionary history of the Bivalvia the mantle became attached peripherally by means of the pallial muscle to the shell. This may or may not have preceeded lateral compression (Yonge, 1957), but following the embayment of the mantle and the development of the ligament, which must have accompanied lateral compression, pallial attachment of the mantle margins bounding the anterior and posterior ends of the mantle isthmus would not occur. In other words, owing to the presence of the ligament, pallial attachment would not be continued from one valve to the other in the depths of the embayments. Thus primitively the extent of pallial attachment in the depths of the two embayments indicated the anterior and posterior limits of the primary ligament. Initially, it is in these regions where the pallial muscles of the two mantle lobes come into contact, as a result of bending of the mantle along the line of the mantle isthmus, that the anterior and posterior adductors develop by the local enlargement and cross fusion of the pallial muscles (Fig. 1A, P.F.). As a consequence of this, the two adductors are inserted on each valve at the anterior and posterior ends of the pallial line (Fig. 1B). In many bivalves, however, the adductors do not occupy this position nor does pallial attachment necessarily extend to the anterior and posterior ends of the primary ligament. The extent of pallial attachment in the anterior and posterior embayments of the mantle, and the position of the adductor muscles, are affected by the form of the shell and the degree of fusion of the outer folds of the mantle margins forming secondary ligament anterior and posterior to the mantle isthmus.

THE ADDUCTOR MUSCLES

The primitive bivalve may or may not have been an equilateral dimyarian in which both marginal increment and the effect of the transverse component (Owen, 1953) decreased symmetrically on either side of the demarcation line (Yonge, 1955 ; replaces " normal axis ", Owen, 1953), but such a bivalve forms a convenient starting point in any discussion on shell form (Figs. 1A and B). The demarcation line (D.L.) intersects the ventral margin at the zone of greatest marginal increment and the generating curve, represented by the valve margin, is circular. It follows that the demarcation line divides each mantle lobe into equal anterior and posterior territories. As already described, in this primitive dimyarian the adductor muscles are situated at each end of the primary ligament (L.P.) and they represent hypertrophied pallial muscles in the depths of the anterior (A.E.) and posterior embayments

(P.E.). This primitive symmetry of the mantle/shell can be altered by changes in the growth gradients around the mantle margin (Owen, 1953). For instance, the single ventrally situated region of greatest marginal increase may be replaced by two regions of maximum marginal increase symmetrically disposed at each end of the ventral margin, and the generating curve, although symmetrical about the demarcation line, now has the form of an ellipse. Such a growth form is represented diagrammatically in Fig. 1 C & D. Each pallial lobe and valve is extended anterior and posterior to the demarcation

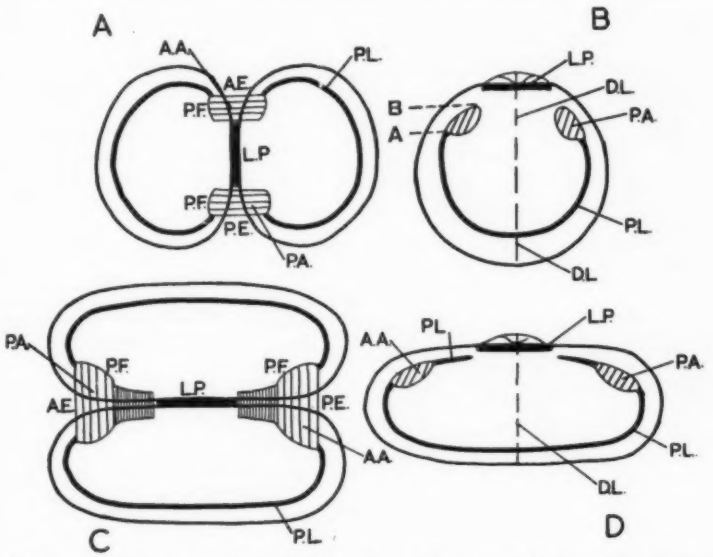


Fig. 1.—Diagrams showing the effect of elongation of the mantle/shell on pallial attachment and the position of the adductor muscles. Figures on the left show the shell spread out and viewed from above, those on the right the internal surface of the right valve. A and B, hypothetical primitive dimyarian ; C and D, hypothetical dimyarian with the mantle/shell elongated anterior and posterior to the demarcation line. A.A., anterior adductor ; A.E., anterior embayment of the mantle ; D.L., demarcation line ; L.P., primary ligament ; P.A., posterior adductor ; P.E., posterior embayment of the mantle ; P.F., cross-hatching, including the adductors, indicates the extent of cross fusion of the pallial muscles in the depths of the two embayments ; P.L., pallial line.

line (D.L.) and, in consequence, there is a corresponding elongation of the dorsal mantle margins of the anterior and posterior embayments, and hence of the regions of cross fusion of the pallial muscles (P.F.). But the regions of the pallial muscles which undergo hypertrophy to form the adductors (A.A., P.A.) are now situated, for obvious functional reasons, some distance from the anterior and posterior ends of the mantle isthmus, although pallial attachment (P.L.), as in the primitive bivalve, still extends to the anterior and posterior ends of the primary ligament (L.P.).

This is essentially the condition in *Lutraria lutraria*, although in this species, in addition to elongation to the mantle/shell on either side of the

demarcation line, the primary ligament is also condensed. As shown in Fig. 2A pallial attachment (P.L.) extends beyond the adductors to near the anterior and posterior ends of the primary ligament (L.P.). In many bivalves the mantle/shell is asymmetrical about the demarcation line, there being a single region of maximum marginal increase situated either anterior or posterior to the demarcation line. Marginal increase is generally greatest posteriorly and it is the posterior region of the mantle/shell which is elongated. This is the case in *Petricola pholadiformis* (Fig. 2C). The posterior margin of the

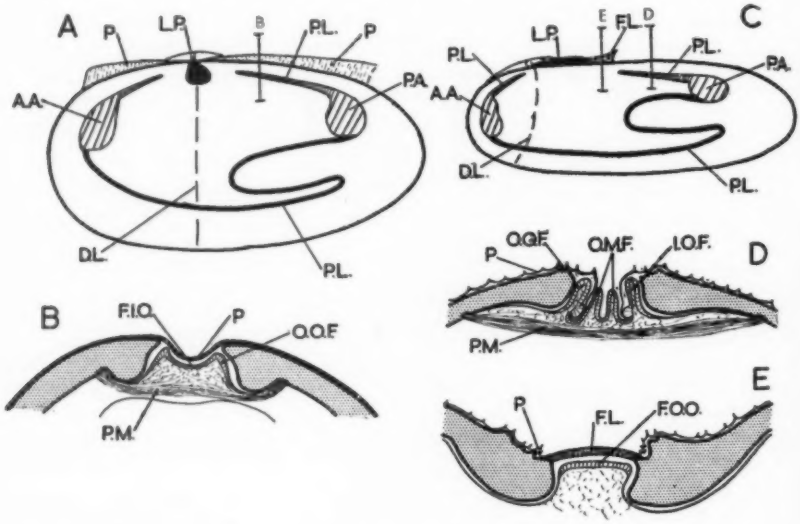


Fig. 2.—Semi-diagrammatic figures showing the relationship between shell form, the ligament, pallial attachment and the position of the adductor muscles in A, *Lutraria lutraria* ; the line B shows the position of a section through the dorsal regions of the valves and mantle margins represented in B ; C, *Petricola pholadiformis*, the lines D and E show the position of the sections represented in D and E. A.A., anterior adductor ; D.L., demarcation line ; F.I.O., fused inner surface of the outer marginal folds ; F.L., fusion layer ; F.O.O., fused outer surfaces of outer marginal folds ; I.O.F., inner surface of outer marginal fold ; L.P., primary ligament ; O.M.F., outer surface of middle marginal folds ; O.O.F., outer surface of outer marginal fold ; P, periostracum ; P.A., posterior adductor ; P.L., pallial line ; P.M., pallial muscles. The cross-hatched region of the pallial line including the adductors represents the region of cross fusion of the pallial muscles in the anterior and posterior embayments.

shell is far removed from the demarcation line (D.L.) and the posterior end of the ligament. For functional reasons the posterior adductor (P.A.) is inserted on the shell near the posterior margin but pallial attachment (P.L.) nevertheless extends anteriorly along the mantle margins of the posterior embayment to the posterior end of the functional ligament. This region of pallial attachment between the adductor and the posterior end of the ligament in *P. pholadiformis* was described by Purchon (1955) as an "accessory dorsal adductor". While it may function as such due to the cross fusion of the

pallial muscles it must be emphasised that pallial attachment in this region represents the normal disposition of the pallial muscles in the posterior embayment of the mantle. It is the position of the adductor which has changed as a result of changes in the form of the mantle/shell (in this case, elongation of the mantle/shell posterior to the demarcation line).

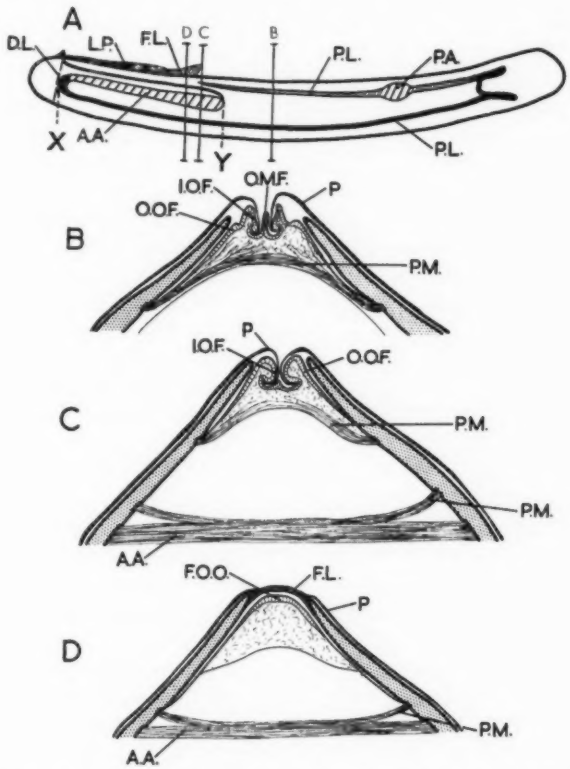


Fig. 3.—A, the right valve of *Ensis ensis* showing the line of pallial attachment, the position of the adductor muscles and the secondary extension of the primary ligament. B, C and D, sections through the dorsal margins of the valves and mantle of *Ensis ensis* at the positions indicated in A. A.A., anterior adductor ; D.L., demarcation line ; F.L., fusion layer ; F.O.O., fused outer surface of outer marginal folds ; I.O.F., inner surface of outer marginal fold ; L.P., primary ligament ; O.M.F., outer surface of middle marginal fold ; O.O.F., outer surface of outer marginal fold ; P, periostracum ; P.A., posterior adductor ; P.L., pallial line ; P.M., pallial muscle. The cross-hatched region of the pallial line, including the posterior adductor muscle, represents the region of cross fusion of the pallial muscles in the posterior embayment of the mantle.

The effect of changes in the form of the mantle/shell on pallial attachment is most marked in the Solenidae (Owen, 1958). In *Phaxus*, *Solen* and *Ensis* (Fig. 3A) the asymmetry of the mantle/shell on either side of the demarcation line (D.L.) is extreme, growth anterior to the demarcation line

being reduced to a minimum (Yonge, 1952 a). Marginal increase occurs almost entirely at the posterior margin resulting in the formation of the characteristically long and blade-like shell. Pallial attachment (P.L.) extends from the posterior end of the functional ligament along the dorsal margins of each shell valve to the base of the siphons. As in *P. pholadiformis*, this pallial attachment along the dorsal margins represents an extension of the region of cross fusion of the pallial muscles in the posterior embayment of the mantle. Hypertrophy of these muscles to form the posterior adductor occurs about two-thirds the distance from the posterior end of the ligament. In all three genera of the Solenidae mentioned above, the anterior adductor muscle (A.A.) is greatly elongated and extends posteriorly beneath the ligament. As already discussed elsewhere (Owen, 1958) this elongation of the anterior adductor is not the result of a simple extension of the posterior margin of the muscle. The effect of the tremendous posterior growth of the mantle/shell in these genera, coupled with minimum growth anteriorly, is to produce an embayment of the line of pallial attachment which extends posterior to the demarcation line. The primitive ventro-dorsal axis (Fig. 1 B, AB) of the anterior adductor is now orientated antero-posteriorly (Fig. 3 A, XY) and pallial muscles, having a separate insertion on the shell from that of the anterior adductor (Fig. 3 C & D) extend anteriorly from the posterior end of the adductor to the anterior end of the ligament (Fig. 3 A).

Yonge (1953 a) has described how the symmetry of the primitive bivalve may be altered either by changes in the form of the mantle/shell affecting the body, or by changes in the body affecting the mantle/shell. Primitively, the two adductors occur at the two ends of the line of pallial attachment. In the bivalves already considered, changes in the positions of the adductors relative to the two ends of the line of pallial attachment are the direct result of elongation of the anterior and/or posterior regions of the mantle/shell. In *Mytilus* (Fig. 4 A) pallial attachment (P.L.) extends not only between the two adductors as in the primitive bivalve, but also along the dorsal margins of the mantle between the posterior adductor (P.A.) and the posterior end of the ligament (L.P.). This dorsal region of pallial attachment was overlooked by Yonge (1953 a) when considering pallial attachment in the Anisomyaria and may have some bearing on the development of a secondary line of pallial attachment in other members of this group (e.g. Pectinacea). The apparent change in the position of the posterior adductor relative to the posterior end of the line of pallial attachment is not in this case the result of a simple posterior elongation of the mantle/shell. Attachment by a byssus has led to changes in the proportions of the body and these changes have secondarily influenced the mantle/shell (Yonge, 1955). The anterior regions of the body are greatly reduced with the result that the umbones and ligament appear to have moved anteriorly, the region of byssus attachment representing a fixed point. Thus in *Mytilus* it is the ligament which can be considered as having moved relative to the posterior adductor, and the pallial muscles between the adductor and the posterior end of the ligament may in consequence represent a secondary extension of the line of pallial attachment. Alternatively, this region may represent an anterior elongation of the region of cross fusion of the pallial

muscles in the posterior embayment of the mantle. In any case, the question of pallial attachment in the Anisomyaria requires further detailed study.

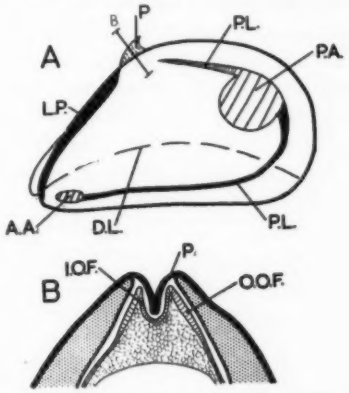


Fig. 4.—A, the right valve of *Mytilus edulis* showing the line of pallial attachment and the position of the adductor muscles ; B, a section through the dorsal margins of the valves and mantle at the position indicated in A. A.A., anterior adductor ; D.L., demarcation line ; I.O.F., inner surface of outer marginal fold in the depth of posterior embayment ; L.P., primary ligament ; O.O.F., outer surface of outer marginal fold ; P, periostracum ; P.A., posterior adductor ; P.L., pallial line.

THE LIGAMENT

It is generally stated that the two adductors of dimyarian bivalves represent the two ends of the line of pallial attachment, but in many bivalves as already described, this does not apply. Changes in the form of the mantle/shell may result in an extension of the regions of cross fusion of the pallial muscles at one or both ends of the mantle isthmus, and, for functional reasons, the adductors are developed some distance from the anterior and posterior ends of the pallial line (Fig. 1). As described by Yonge (1953 b), in the evolution of the Bivalvia, bending of the mantle along the line of the mantle isthmus must have been followed by fusion of the mantle margins in the anterior and posterior embayments. Initially, this fusion of the mantle margins must have involved the inner folds only but in the great majority of bivalves the middle and frequently the outer marginal folds are also involved (Yonge, 1957). From an examination of a variety of bivalves it has been concluded that where fusion of the mantle margins anterior and posterior to the mantle isthmus i.e. within the embayments, involves, (1) the inner folds only (Type A, Yonge, 1957) ; (2) the inner and middle folds (Types B and C) ; (3) the inner and middle folds together with the inner surfaces of the outer folds (Type C) ; attachment of the mantle to the shell by pallial muscles is retained and the pallial line extends to either end of the primary ligament. Where the outer surfaces of the outer folds are also involved (Type D), as is the case when the primary ligament is secondarily extended by fusion layer, there is an accompanying loss of pallial attachment and the pallial line now extends to the anterior and posterior limits of the fusion layer.

This connexion between the degree of fusion of the mantle margins and pallial attachment is best illustrated by a series of examples. The degree of fusion of the mantle margins has been determined from sections and for convenience the examples are, as far as possible, those used in discussing the effect of shell form on the position of the adductor muscles. In *Petricola pholadiformis* fusion of the mantle margins between the base of the exhalent siphon and the posterior end of the functional ligament involves the inner folds together with the inner surfaces of the middle folds. As shown by the presence of the pallial line on the internal surface of the valves (Fig. 2 C, P.L.) there is pallial attachment of these fused mantle margins to the shell valves. As already described, the line of pallial attachment in this region represents an extension of the region of cross-fusion of the pallial muscles in the posterior embayment of the mantle ; the adductor muscle is now situated at the posterior end of the elongated embayment. In contrast to the primitive condition, however, pallial attachment does not extend to the posterior end of the primary ligament (L.P.). In *P. pholadiformis* the posterior end of the primary ligament is secondarily extended by fusion layer (F.L.), a result of the fusion of the outer surfaces of the outer folds of the mantle margins posterior to the mantle isthmus (Figs. 2 C and E). This secondary extension of the primary ligament by way of fusion layer is accompanied by a loss of pallial attachment and the pallial line ends at the posterior margin of the fusion layer. Conditions are essentially similar in *Ensis ensis* (Fig. 3) and all members of the Solenidae (Owen, 1958). Pallial attachment in the very elongated posterior embayment of *E. ensis* extends beneath the fused inner folds and inner surfaces of the middle folds (Fig. 3 B) to the posterior end of the fusion layer (Fig. 3 A). As in *P. pholadiformis*, extension of the primary ligament by fusion layer has been accompanied by the loss of pallial attachment. In *Lutraria lutraria* fusion of the mantle margins anterior and posterior to the ligament (Fig. 2 B) involves for the most part the inner and middle folds together with the inner periostracal-secreting surfaces of the outer folds (Type C) and the valves are joined dorsally by periostracum (P). As shown in Figure 2A, the line of pallial attachment (P.L.) extends beyond the adductors to near the anterior and posterior ends of the ligament. Thus fusion of the *inner* surfaces of the outer folds is not accompanied by the loss of pallial attachment.

In *Astarte sulcata* the adductor muscles are inserted at each end of the line of pallial attachment although the adductors are some distance from the anterior and posterior ends of the primary ligament (Fig. 5 A). Anterior and posterior to the primary ligament the dorsal margins of the valves are firmly joined by a non-calcareous secretion which appears to be similar to the thick periostracum covering the external surface of the valves. Sections through this region (Fig. 5 B) show the mantle margin between the two valves as a slender finger-like projection (F.O.O.) which can only be interpreted as representing the fused outer surfaces of the outer folds (Type D), and as such, it secretes a thick pad of fusion layer (F.L.) joining the two valves and continuous on each side with the periostracum (P). Thus, the primary ligament of *Astarte* (Fig. 5A ; L.P.) is extended anteriorly and posteriorly by fusion layer

and there is an accompanying loss of pallial attachment in the anterior and posterior embayments of the mantle. In *Myadora ovata* the primary ligament is condensed but the line of pallial attachment ends at the adductor muscles (Fig. 5C). The two shell valves appear to be joined dorsally, anterior and posterior to the primary ligament by periostracum but sections show the mantle margin in this region to be a simple, laterally flattened crest of tissue projecting between the valve margins (Fig. 5D ; F.O.O.). As in *Astarte*, this marginal crest is interpreted as representing the fused outer surfaces of the outer folds of

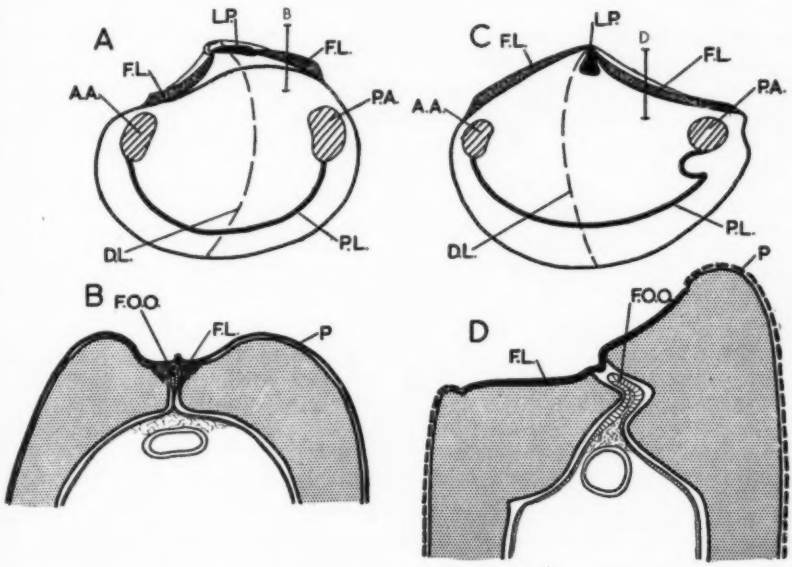


Fig. 5.—The right valves of A, *Astarte sulcata* ; C, *Myadora ovata*, showing secondary extension of the primary ligament, the pallial line and the position of the adductor muscles. B and D sections through the dorsal margins of the valves and mantle of *Astarte* and *Myadora* respectively. The position of the sections is shown in figures A and C. A.A., anterior adductor ; D.L., demarcation line ; F.L., fusion layer ; F.O.O., fused outer surface of outer margin folds ; L.P., primary ligament ; P, periostracum ; P.A., posterior adductor ; P.L., pallial line.

the mantle margins in the anterior and posterior embayments, and the two valves are joined by fusion layer (F.L.). Unlike *Astarte*, the fusion layer in *Myadora* extends over the external surface of the inturned dorsal regions of the valves. Moreover, while the periostracum covering most of the external surface of the valves has a characteristic " cellular " or honeycomb-like appearance, the fusion layer is a continuous sheet (Fig. 5D). It is probable that in related bivalves, e.g. the Lyonsiidae, the two valves are united dorsally by fusion layer and not by periostracum as described by Yonge (1952 b, 1957).

Anodonta cygnea provides one of the best examples of the loss of pallial attachment which accompanies the secondary extension of the primary

ligament by fusion layer as a result of the fusion of the outer surfaces of the mantle margins at either end of the mantle isthmus. The line of pallial attachment ends at the two adductors which are inserted on the shell some distance from the anterior and posterior ends of the primary ligament (Fig. 6A). In this species, the primary ligament (L.P.) is secondarily extended at each end by what is obviously fusion layer (F.L.). Sections anterior (Fig. 6B) and posterior (Fig. 6C) to the primary ligament show that the epithelium of the fused outer surfaces of the outer marginal folds (F.O.O.) secretes non-calcareous

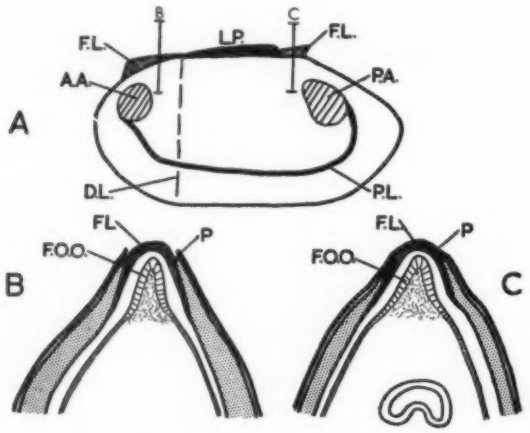


Fig. 6.—A, the right valve of *Anodonta cygnea* showing the pallial line, position of the adductors and secondary extension of the ligament. B and C, sections through the dorsal margins of the valves and mantle at the positions indicated in A. A.A., anterior adductor; D.L., demarcation line; F.L., fusion layer; F.O.O., fused outer surfaces of outer marginal folds; L.P., primary ligament; P, periostracum; P.A., posterior adductor; P.L., pallial line.

fusion layer which extends on each side beneath the outer calcareous layer of the valves. This outer calcareous layer of the valves is secreted by the outer surfaces of the outer fold prior to their fusion anterior and posterior to the mantle isthmus.

Finally, mention must be made of the relationship between pallial attachment and the ligament in *Mytilus edulis*. In this species there is no fusion of the outer secretory folds of the mantle margins at either end of the ligament. Pallial attachment extends from the anterior adductor at the anterior end of the ligament, round the periphery of each pallial lobe, to the *posterior margin* of the periostracum which "extends" the posterior end of the ligament (Fig. 4A). This "extension" of the ligament of *M. edulis* by periostracum is not, however, the result of fusion of the inner surfaces of the outer marginal folds posterior to the mantle isthmus. It is secreted at the posterior margin of the mantle isthmus by the inner surface of the outer fold where this bends around from one valve to the other. In those species where, at either end of the ligament, the two valves are joined by periostracum as a result of the

fusion of the inner surfaces of the outer folds (e.g. *Lutraria, Mya, Pharella*), these folds are parallel to the valve margins and the mantle is attached to the shell by pallial muscles. But where the outer marginal fold bends around from one valve to the other at the anterior and posterior ends of the mantle isthmus, the outer fold is at right angles to the valve margins, and as a result, there is no pallial attachment. Care must be taken to distinguish between *fusion* of the folds of the mantle margins, and the bending around of these folds from one valve to the other in the depths of the two embayments.

Sufficient examples have now been described to show that where the inner surfaces of the outer folds are fused and the two valves joined by periostracum, pallial attachment is retained, but if the outer surfaces of these folds are also involved then pallial attachment is lost. It should, therefore, be possible to determine the type of secondary extension of the primary ligament (i.e. periostracum or fusion layer) without sectioning the specimen, by studying the extent of the pallial line on the internal surface of the valves.

ACKNOWLEDGMENTS

I would like to thank Professor C. M. Yonge, C.B.E., F.R.S., for his continued interest and valuable help. I am also indebted to the Royal Society for the award of the John Murray Travelling Studentship. A study of various bivalves collected in New Zealand and Singapore led to the observations made in this paper.

SUMMARY

Examples are given to show how in the Bivalvia, (a) changes in the form of the mantle/shell may affect the position of the adductor muscles, and (b) secondary extension of the primary ligament may limit the extent of pallial attachment in the anterior and posterior embayments of the mantle.

Secondary extension of the ligament may take place by periostracum or by fusion layer but it is probable that only fusion layer is of functional significance. Where the outer surfaces of the outer folds of the mantle margins anterior and posterior to the mantle isthmus are fused, as in the formation of fusion layer, there is an accompanying loss of pallial attachment and in most, if not all bivalves, the pallial line extends to the anterior and posterior ends of the functional ligament whether this consists of primary ligament only, as in *Mytilus edulis*, or of primary ligament secondarily extended by fusion layer, as in *Anodonta cygnea*. The extent of the pallial muscles in the anterior and posterior embayments is therefore of use in distinguishing between (a) fusion of the *inner* surfaces of the outer folds (i.e. when the two valves are joined by *periostracum*) and (b) fusion of the *outer* surfaces of the outer folds (i.e. when the two valves are joined by *fusion layer*).

Elongation of the mantle/shell on either side of the demarcation line results in a corresponding extension of the region of cross fusion of the pallial muscles in the anterior and posterior embayments. For functional reasons the adductor muscles develop near the anterior and posterior margins of the

shell and as a result, in many bivalves pallial attachment extends beyond the adductors to the anterior and posterior ends of the functional ligament. This feature of pallial attachment in the Bivalvia appears to have been overlooked.

REFERENCES

Beedham, G. E. (1958). Observations on the mantle and shell of the Lamellibranchia. II. The non-calcareous component of the shell. *Quart. J. micr. Sci.* (in the press).

Owen, G. (1953). The shell in the Lamellibranchia. *Quart. J. micr. Sci.* **94,** 57.

Owen, G. (1958). Observations on the Solenacea with reasons for excluding the Family Glaucomyidae. *Phil. Trans.* (B) (in the press).

Owen, G., Trueman, E. R. & Yonge, C. M. (1953). The ligament in the Lamellibranchia. *Nature, Lond.* **171,** 73.

Purchon, R. D. (1955). The functional morphology of the rock-boring lamellibranch *Petricola pholadiformis* Lamarck. *J. mar. biol. Ass., U.K.* **34,** 257.

Yonge, C. M. (1947). The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans.* (B) **232,** 443.

Yonge, C. M. (1952 a). Studies on Pacific coast molluscs. IV. Observations on *Siliqua patula* Dixon and on evolution within the Solenidae. *Univ. Calif. Publ. Zool.* **55,** 439.

Yonge, C. M. (1952 b). Studies on Pacific coast molluscs. V. Structure and adaptations in *Entodesma saxicola* (Baird) and *Mytilimeria nuttallii* Conrad. *Univ. Calif. Publ. Zool.* **55,** 439.

Yonge, C. M. (1953 a). The monomyarian condition in the Lamellibranchia. *Trans. Roy. Soc. Edinb.* **62,** 443.

Yonge, C. M. (1953 b). Form and habit in *Pinna carnea* Gmelin. *Phil. Trans.* (B) **237,** 335.

Yonge, C. M. (1955). Adaptation to rock boring in *Botula* and *Lithophaga* (Lamellibranchia, Mytilidae) with a discussion on the evolution of this habit. *Quart. J. micr. Sci.* **96,** 383.

Yonge, C. M. (1957). Mantle fusion in the Lamellibranchia. *Pubbl. Staz. Zool. Napoli* **29,** 151.

NOTICE

["Proceedings", **Vol. 131, Part 3,** was published on the 1st November, 1958.]

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C.4.

INSTRUCTIONS TO AUTHORS.

Two volumes of the Society's " Proceedings " each of four parts, are issued annually, and the " Transactions " at irregular intervals. Papers for publication should be addressed to: The Editor, Zoological Society of London, Regent's Park, London, N.W.1. Papers forwarded for publication are understood to be original works and to be offered to the Zoological Society alone unless the contrary is stated. The copyright becomes the property of the Society when papers are accepted. The Scientific Committee draws the attention of authors submitting papers for publication by the Society to the following regulations. If the conditions are not observed, papers will be returned.

MSS. submitted for publication must be type-written with double spacing between the lines and good margins, and must be in final form for printing. They must be typed on one side only of each sheet, and the sheets must be numbered. Papers must include a **Table of Contents** and a **Summary** containing a succinct account of the subject, results obtained and conclusions. The summary must not exceed one-twentyfifth of the text in length. The positions for text-figures and tables must be indicated in pencil in the margin. The metric system should be used for all measurements. Footnotes are to be avoided.

References in the text must be cited by giving the author and date, e.g. " Smith (1957) stated . . . " and the complete references arranged in alphabetical order of the authors' names at the **end of the paper.** They must contain the following information, in the order given: (1) The author's name(s) and initials(s). If there is more than one author the ampersand (&) not the word " and " must be used between the last and the penultimate names. (2) The publication date of the paper, in brackets. If reference is made to more than one paper by the same author(s) published in a single year, the suffixes a, b, etc. should be used, e.g. (1951 a). (3) The full title of the paper. Only the first word, except proper names, may have a capital letter. Titles in German have capitals as in the original journal. (4) The title of the journal abbreviated according to the " World list of scientific periodicals ". (5) The volume number in arabic numerals without the prefix " vol." and the number of the first page in arabic numerals, without the prefix " p.". If the journal has appeared in more than one series the series number must appear in brackets before the volume number, e.g. (3), (n.s.), (B).

Where the reference is a separate book the title must be underlined and the place of publication given.

References thus appear as follows:—

PARRINGTON, F. R. (1956). The patterns of dermal bones in primitive vertebrates. *Proc. zool. Soc. Lond.* **127**, 389.

COWLES, R. B. (1956). Sidewinding locomotion in snakes. *Copeia* **1950**, 211.

ROMER, A. S. (1956). *Osteology of the reptiles.* Chicago.

GREEN, J. (1956). Variation in the haemoglobin content of *Daphnia*. *Proc. roy. Soc.* (B) **145**, 214.

Illustrations, particularly plates, are expensive and should be kept to the minimum. It is important that a scale, in either centimetres, millimetres or microns should appear on all drawings and photographs. The size of the original must *not* be shown by a multiplying factor, e.g. ×120 or ×1/10 because such factors may be altered in the process of block-making.

COPYRIGHT.—Any communication made to the Society will, if accepted for publication, become the property of the Society, and will not be returned to the author, except for the purpose of comparison with the proof when set up in type. The author assigns to the Society the copyright of the text and illustrations in consideration of their paying the cost of production and granting twenty-five separate copies free of charge. The Scientific Committee is always ready to give authors who apply for it permission to reproduce matter that they have contributed to the Society's " Proceedings " and " Transactions ".

A leaflet giving fuller details of the Society's instructions to authors may be obtained gratis on application to the Librarian and Clerk of Publications.

LIST OF CONTENTS

VOL. 131

PART 4 (pp. 487–648)

Page

ASHTON, E. H. and OXNARD, C. E.
Variation in the maxillary nerve of certain mammals. (3 figures) 607

ATKINS, D.
A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. (1 plate and 14 figures) 559

DAVID, P. M.
A new species of *Eukrohnia* from the Southern Ocean with a note on fertilization. (3 figures) 597

OWEN, GARETH
Shell form, pallial attachment and the ligament in the Bivalvia. (6 figures) 637

OXNARD, C. E. *See* ASHTON, E. H.

PAUL, A. R.
Eastbourne marine shore fauna. (1 figure) 527

PURCHON, R. D.
The stomach in the Eulamellibranchia ; Stomach Type IV. (14 figures) 487

TYLER, MICHAEL J.
On the diet and feeding habits of the Edible frog (*Rana esculenta* Linnaeus). (5 figures) 583

WEBB, J. E.
On a collection of lancelets from the Gambia, with a description of a new species of *Branchiostoma*. (2 figures) 627

TITLE PAGE, LIST OF CONTENTS AND INDEX

NOTICE.

"Proceedings" Vol. 131, Part 3, was published on 1st November, 1958.